Population biology and ecology of albatrosses on Macquarie Island: implications for conservation status

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Statement of Originality

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution. To the best of my knowledge, this thesis contains no material previously published or written by another person, except where due acknowledgement is made in the text.

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Aleks Terauds 25/2/03

Grey-headed albatross breeding on West Rock, Macquarie Island

Abstract

Four species of albatross breed on Macquarie Island, a small subantarctic island located halfway between Australia and Antarctica. Three of these species (Wandering albatrosses (*Diomedea exulans*), Black-browed albatrosses (*Thalassarche melanophrys*) and Grey-headed albatrosses (*Thalassarche chrysostoma*)) are particularly at risk from elevated mortality levels due to the small size of the breeding populations. Wandering albatrosses have the smallest breeding population of approximately ten breeding pairs each year (total breeding population estimated as 19 breeding pairs), followed by Black-browed albatrosses with approximately 40 breeding pairs each year (total breeding population 38-45 pairs) and Grey-headed albatrosses, with 65-75 breeding pairs each year (total breeding population 100-120 breeding pairs). Light-mantled sooty albatrosses (*Phoebetria palpebrata*) are more abundant on Macquarie Island (total breeding population estimated at 1500-1800 breeding pairs) and this population represents around 5-10% of the global population.

Worldwide declines of many albatross populations were documented in the late 1980's and 1990's and in most cases this was attributable to elevated mortality due to interactions with long-line fisheries. In response these concerns, and in an attempt to address the paucity of data on albatrosses breeding on Macquarie Island, a long-term study into the four species was initiated in 1994. The main aims of this study were to determine the conservation status of each species on Macquarie Island, identify long-term population trends and determine the factors responsible for these trends. To achieve these aims three main aspects were investigated: 1) Population dynamics - involving censuses and identification of breeding birds and collation of historical data to examine longer-term population trends and survivorship; 2) Breeding biology - where breeding success, breeding frequency and attendance patterns were investigated and 3) Foraging ecology - involving satellite tracking of Black-browed and Grey-headed albatrosses and a more intensive investigation of the provisioning regime of Light-mantled sooty albatrosses using automatic weighing nests and VHF transmitters. Oceanographic data (Chlorophyll A, Sea Surface Temperature and Sea Surface Height Anomaly) were also obtained and utilised in the analyses of trends in breeding success and satellite tracking.

This thesis describes and synthesises data collected from 1994 to 2001 (seven field seasons). These data are discussed both in the context of the threat of long-line fishing and also in the global context. Macquarie Island is the only Australian breeding site of these four albatross species and prior to the current study very limited information was available on these

breeding populations. The current study enabled comparisons to be made with other breeding populations of these species at other subantarctic locations (e.g. Iles Crozet and Kerguelen, South Georgia, New Zealand and Marion Island) where long-term studies of these species and close conspecifics have been conducted.

The entire breeding populations of the Wandering, Black-browed and Grey-headed albatrosses on Macquarie Island were monitored each year, while a sub-sample of the Light-mantled sooty albatrosses was investigated. All breeding populations were relatively stable between 1994/95 and 2000/01. Prior to this, Wandering albatrosses showed the most variation in both breeding numbers and survivorship. This population was nearly extirpated by 'sealers' at the turn of the century and following their departure from Macquarie Island, breeding numbers slowly increased to peak in the mid 1960's at around 45-50 breeding pairs. Following this increase, breeding numbers started to decline again, reaching a low of 2-3 breeding pairs in the mid-1980's and slowly rising to its current level of 19 breeding pairs in the mid-1990's. The major decline from the 1960's to the 1980's was largely attributable to a sharp decrease in fledgling survivorship and low adult survivorship. These survivorship declines coincided with the advent and proliferation of long-line fisheries, particularly in the Indian Ocean.

The Black-browed and Grey-headed albatross breeding populations appeared relatively stable between the late 1970's and the advent of the current study, with some evidence of an increase in breeding numbers. Survivorship of these two species did not vary significantly over this time period. There are limited data on breeding numbers of these two species prior to the 1970's; however a small Black-browed breeding population in the north of the island did decline significantly throughout the 1960's and 1970's and was extinct by the early 1980's.

Between 1994/95 and 2000/01 Wandering albatrosses had the highest and most variable breeding success of all albatrosses on Macquarie Island (59.7 ± 6.9 (s.e) %) followed by Grey-headed albatrosses (55.3 ± 4.0 %), Light-mantled sooty albatrosses (50.8 ± 1.9 %) and Black-browed albatrosses (46.1 ± 3.6 %). Chick mortality was generally low for all species, and most variation in overall breeding success could be attributed to variation in hatching success. The inter-annual variation in breeding success of Black-browed albatrosses was correlated with chlorophyll A levels, breeding success of Light-mantled sooty albatrosses was correlated with sea surface temperature and the breeding success of Grey-headed albatrosses was correlated with the intensity and location of sea surface height anomalies. Breeding birds

were also classified into 'top' (successful > 65% breeding attempts) and 'bottom' breeders (successful < 35% breeding attempts) and used to further examine variation in breeding frequency and attendance patterns.

The breeding frequencies of albatrosses on Macquarie Island are consistent with those found in other studies on the same species breeding at different locations. Wandering albatrosses showed the strictest adherence to the biennial pattern and most Grey-headed and Light-mantled sooty albatrosses also followed this pattern of breeding frequency. Approximately 16-20% of the successful breeders from the latter two species deferred breeding for more than two years with most of this deferral attributable to birds not attaining adequate 'condition' in the non-breeding season. Black-browed albatrosses followed an annual breeding pattern and most deferral of breeding in this species (approximately 6% successful birds) was also likely to be related to the attainment of breeding condition in the non-breeding period.

The mean shift lengths of the four species during incubation were significantly different and reflected the primary foraging strategy of each species. Black-browed albatrosses had the shortest shift length (3.1 ± 0.27 (s.e) days), followed by Grey-headed albatrosses (5.0 ± 0.19 days), Wandering albatrosses (8.8 ± 0.44 days) and Light-mantled sooty albatrosses (10.5 ± 0.4 days). Shift length during this time period was variable, particularly for Black-browed albatrosses, indicating that breeders were foraging different distances away from Macquarie Island, or that some were foraging more efficiently than others. Wandering albatrosses and Light-mantled sooty albatrosses had the most similar mean shift lengths during incubation and it is likely that these two species forage mostly in distant pelagic waters during this period. Shift lengths of the four species during the brood-guard period were significantly shorter and less variable suggesting that all species utilise resources close to Macquarie Island during this stage of the breeding cycle.

The foraging distributions of five Grey-headed and three Black-browed albatrosses were examined during incubation and the brood-guard stage via satellite telemetry. Most foraging trips of Black-browed albatrosses were within 100 km of Macquarie Island and concentrated over the ridge system to the north and south of the island. However, one breeding bird travelled over 1000 km to the south to forage suggesting that this species does utilise oceanic resources distant from the breeding colony. Grey-headed albatrosses foraged primarily in oceanic waters in the Polar Frontal Zone. Most foraging activity of this species occurred 1000-1500 km east south-east of Macquarie Island, south-east of the Campbell Plateau and was usually concentrated around the edges of Sea-Surface Height Anomalies.

The provisioning strategies of Light-mantled sooty albatross were also examined. Provisioning regimes were investigated at two locations over two breeding seasons. There were no significant differences between years with adults generally undertaking a long foraging trip (5-11 days) followed by 3-4 daily feeding trips. As a result the chicks were fed on average every 1.4 days to 1.6 day. Chicks fasted for up to 10 days at a time if the foraging trips of both parents were synchronised and chicks were often fed 2-3 times in one day when both parents were foraging close to Macquarie Island. The total amount of feed each chick received during its unattended life on the nest averaged 37.5 kg and the mean meal size was 518 grams and ranged from 160 g to 1.05 kg feeds in a single feed.

This study has significantly increased our understanding of the conservation status and biology of these breeding populations on Macquarie Island. Factors that are likely to contribute to population changes in the future have been identified and differences between these breeding populations and populations at other subantarctic locations were documented. In general, the Macquarie Island albatross populations appeared more similar to Indian Ocean populations (e.g. Iles Crozet, Kerguelen and Marion Island) and New Zealand than those in the Atlantic Ocean (eg South Georgia). The monitoring carried out as part of this study is integral in focusing effort, both national and international, on the formulation of effective conservation initiatives that will assist in the long-term survival of these species.

Acknowledgements

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Chapter 1 - General Introduction

1.1 BACKGROUND

Albatrosses (Family Diomedeidae) are largest members of the petrel family (Order Procellariiforme) and are comprised of 24 distinct taxa in four genera (see review in Robertson and Nunn 1998). They are long lived, generally pelagic seabirds that are characterised by a late onset of sexual maturity, single egg clutches, low breeding success, extreme longevity and naturally high adult survivorship (Warham 1990; Russell 1999). Few species (terrestrial or marine) exhibit such extreme 'k-selected' life history attributes and the evolution of such traits are likely to be associated with maximising lifetime reproductive success in the harsh but stable marine and terrestrial environments that these seabirds inhabit (Lack 1968; Boggs 1992; Stearns *et al.* 2000). A consequence of these life history characteristics is that albatrosses, both at population and species levels, are exceptionally vulnerable to 'unnaturally' elevated mortality levels (Gales 1993; Alexander *et al.* 1997). These life history characteristics also mean that the recovery of populations exposed to elevated mortality levels is slow, particularly if the threat is ongoing.

Albatrosses typically breed in the higher latitudes of the world's hemispheres and with the exception of Waved (*Phoebastria irrorata*), Black-footed (*Phoebastria nigripes*) and Laysan albatrosses (*Phoebastria immutabilis*), all inhabit oceanic islands in temperate regions. The number and intensity of studies on albatrosses have increased since the late 1970's and 1980's when the first signs of declining albatross populations in the Southern Ocean were identified. Declines in Wandering albatross (*Diomedea exulans*) populations were first reported on South Georgia (Croxall 1979), Macquarie Island (Tomkins 1985b), Iles Crozet (Jouventin *et al.* 1984) and Possession Island (Weimerskirch and Jouventin 1987). The latter two studies were of the first to link the observed declines to increased mortality due to long line fisheries. Mortality of albatrosses interacting with driftnet fisheries in the northern hemisphere was documented as early as the 1960's with Black-footed, Laysan and Short-tailed albatrosses all being reported as being caught and killed in large numbers throughout the 1960's and 1970's (Fisher and Fisher 1972; Robbins and Rice 1974; King *et al.* 1979 cited in Brothers *et al.* 1999).

More recently, studies have conclusively documented the decline of albatross populations throughout the southern hemisphere (see review in Gales 1998). Breeding locations at which these declines have been recorded include South Georgia (Croxall *et al.* 1990; Prince *et al.*

1994; Croxall *et al.* 1998), Iles Crozet and Iles Kerguelen (Weimerskirch *et al.* 1998, Weimerskirch *et al.* 1997a), Amsterdam Island (Inchausti and Weimerskirch 2001, Marion Island (Nel *et al.* 2002a) New Zealand (Waugh *et al.* 1999b; Walker and Elliott 1999; Sagar *et al.* 1999), and Macquarie Island (de la Mare and Kerry 1994). In all of these studies, the declines were associated with increased mortality due to interactions of the albatrosses with long-line fisheries operations (Gales 1998).

Long-line tuna fisheries were originally identified as the main source of albatross mortality and the distribution of these fleets was widespread throughout temperate latitudes of the southern hemisphere throughout the 1970's and 1980's (Tuck and Bulman 2001). The potential scale of the impact of tuna long-line fisheries on albatrosses was highlighted by the seminal work of Brothers (1991), and subsequent studies provided more data on the extent and nature of the interactions (Murray *et al.* 1993, Klaer *et al.* 1995; Klaer and Polacheck 1997, Gales *et al.* 1999, Brothers *et al.* 1999). In two comprehensive reviews of the conservation status and threats of albatross populations worldwide, Gales (1993) and Gales (1998) described long-line fishing as the most serious threat to the survival of albatross populations. The relatively recent advent of a large-scale fishery for Patagonian Toothfish (*Dissostichus eleginoides*) in Southern Ocean waters also presents a significant threat to albatrosses foraging in these areas (Croxall and Prince 1996; Cherel, 1996; Moreno *et al.* 1996; Robertson and Weinecke 2000; Nel et al. 2002a; Nel et al 2002b; Ryan and Boix-Hinzen 1999)

The declines reported in other Southern Ocean albatross populations and the increasing concerns over the number of albatrosses killed as a result of long-line fisheries prompted the initiation of a comprehensive long-term study of the population trends, breeding biology and foraging ecology of the albatrosses on Macquarie Island. In addition to concerns over elevated mortality, the study was also designed to complement albatross research in the global context. The population status of many breeding population worldwide has been established (Gales 1998) and the inclusion of the little studied Macquarie Island breeding populations in this global pool of data was considered critical, particularly in light of the small and vulnerable breeding populations. Research strategies were formulated accordingly throughout the study and aspects for which there existed little or no data were the primary focus. A full description of the global context of the results of the present study is presented in the General Discussion (Chapter 9). The present study began in the summer season of 1994/95 and was initiated by Rosemary Gales and Nigel Brothers of the Nature Conservation Branch, Department of Primary Industry, Water and Environment (DPIWE), Tasmania.

1.2 SPECIES AND STUDY SITE.

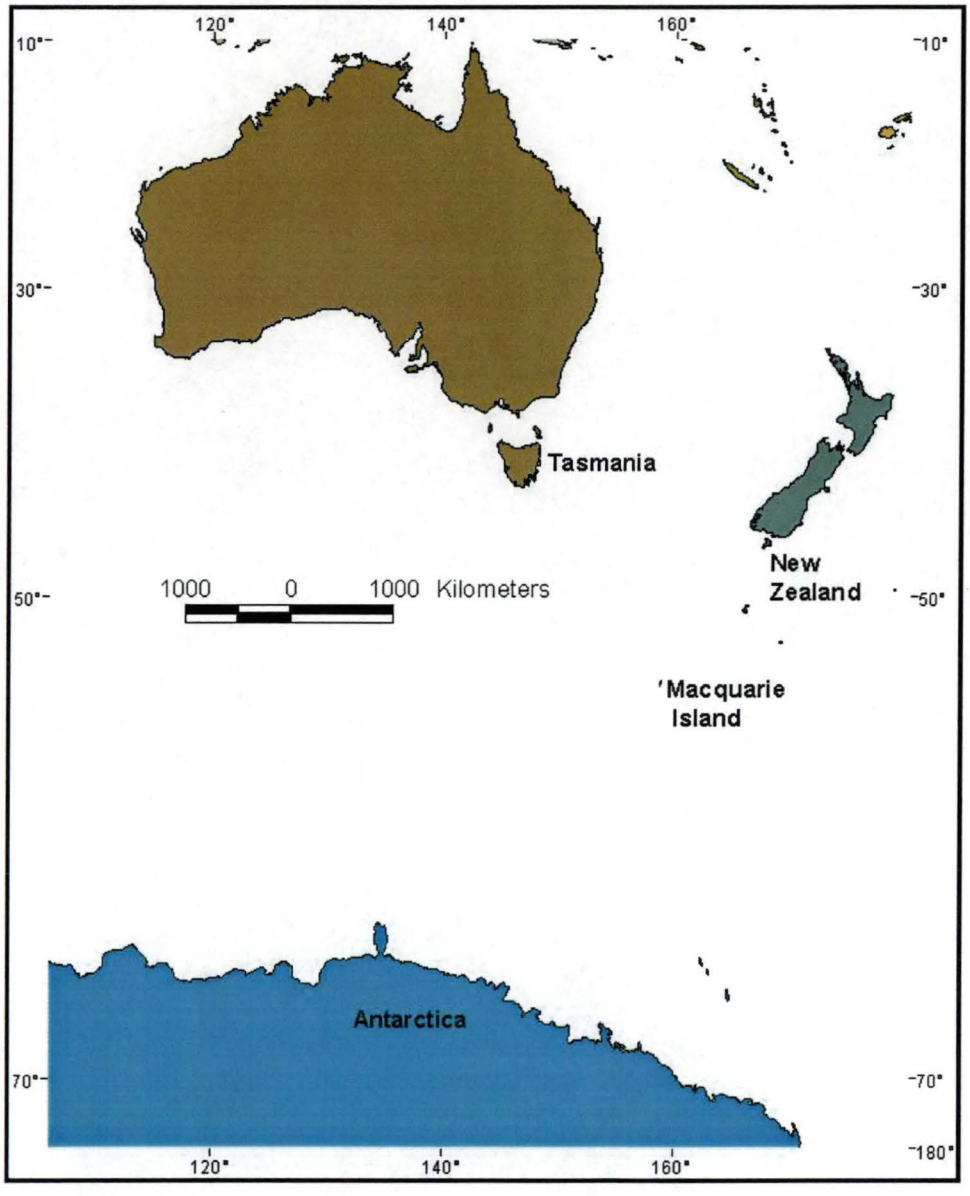
Macquarie Island is a small isolated subantarctic island situated approximately 1500 km south of Tasmania (Figure 1.1) at 54°30' S and 158°55'E. It is a Tasmanian Nature Reserve, an International Biosphere Reserve and a World Heritage Area and managed by the Department of Primary Industries, Water and Environment (DPIWE), Tasmania. Four species of albatrosses breed on Macquarie Island and all have been described as being caught and killed on long-line fishing vessels (Gales 1993; de la Mare and Kerry 1994; Gales 1998). Three of these species; Wandering albatrosses (*Diomedea exulans*), Black-browed albatrosses (*Thalassarche melanophrys*) and Grey-headed albatrosses (*Thalassarche chrysostoma*) are particularly at risk due to the small size of the breeding populations on Macquarie Island (<100 pairs annually - Table 1.1). Light-mantled sooty albatrosses (*Phoebetria palpebrata*) are more abundant on Macquarie Island (*ca* 1100 annual breeding pairs); however, this population represents around 5 % of the global population (Gales *et al.* 1998) and little is known about the impact of fisheries on this species. Studies into the taxonomy of these species are ongoing (e.g. Burg 2000) and the taxonomy used throughout this thesis follows Robertson and Nunn (1998). The conservation status of each species under International Union for Conservation of Nature (IUCN), national and state criteria are listed in Table 1.1:

Table 1.1
Number of breeding pairs and conservation status listing of Wandering, Black-browed, Grey-headed and Light-mantled sooty albatrosses [1]

Species	Number of annual breeding pairs		Population status listing		
	Macquarie Island	Global	IUCN	National	State
Wandering albatross	7-15	8500	Vulnerable	Vulnerable	Endangered
Black-browed albatross	38-45	680 000	Near Threatened	Protected	Endangered
Grey-headed albatross	65-80	92 300	Vulnerable	Vulnerable	Endangered
Light-mantled sooty albatross	~1100	21 600	Near Threatened	Protected	Vulnerable

1 - sourced from the current study, Environment Australia (2001a), Birdife International (2001a, b)

Figure 1.1
Location of Macquarie Island



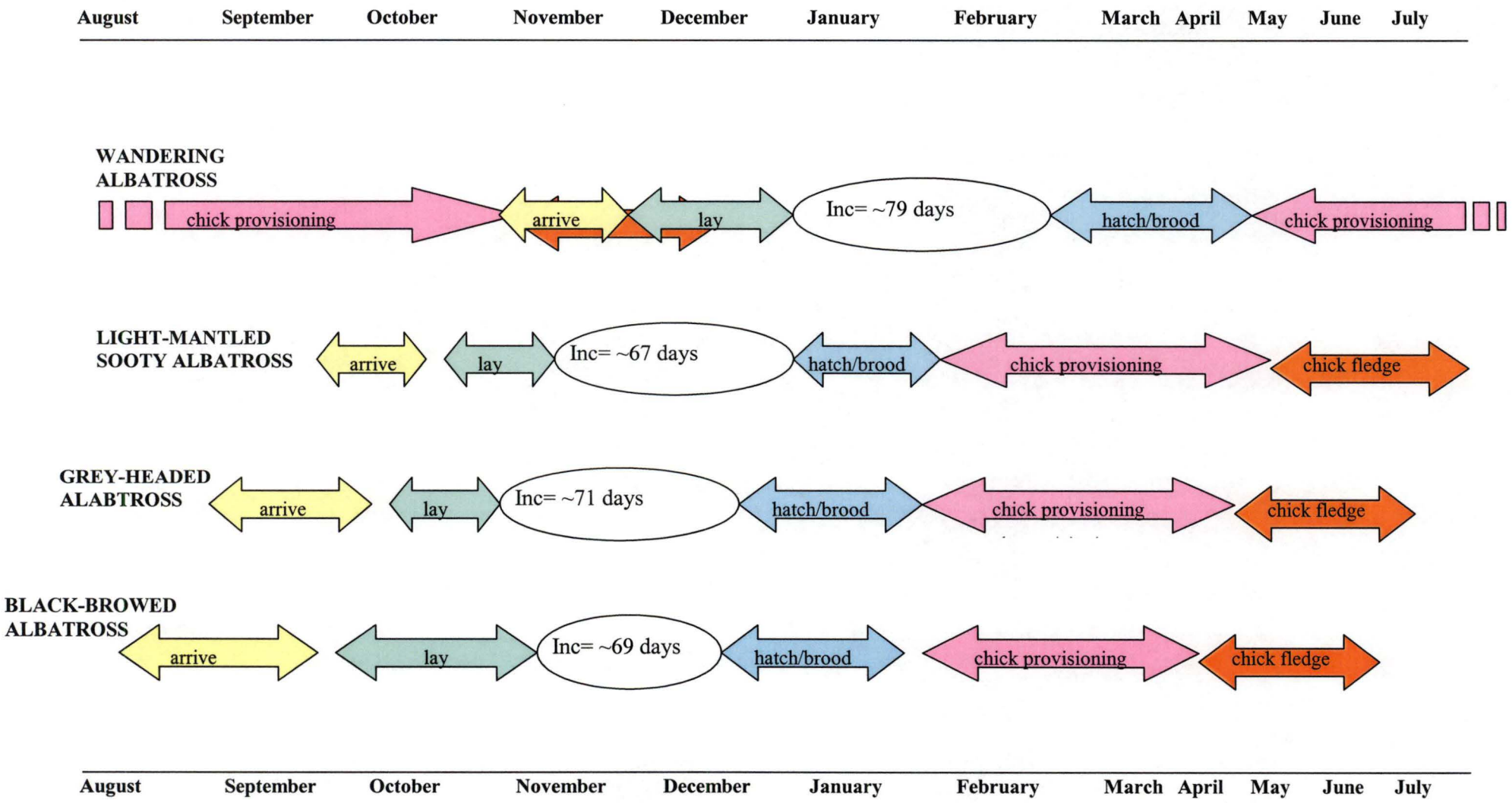
The small and vulnerable breeding populations of Black-browed and Grey-headed albatrosses are confined to the south-western corner of Macquarie Island (Figure 1.2) and approximately 38-44 pairs of Black-browed albatrosses and 65-80 pairs of Grey-headed albatrosses breed in this area each year. It has been estimated that there are 140 breeding pairs of Black-browed albatrosses on Bishop and Clark Islets (Nigel Brothers, unpublished data), approximately 37 km to the south of Macquarie Island. The majority of Wandering albatrosses also breed in the south-western corner of Macquarie Island, although a small number (approximately four pairs in total) also breed on the north-western coastal flats (Figure 1.2). The total breeding population of Wandering albatross on Macquarie Island is approximately 19 breeding pairs, with seven to twelve pairs usually breeding each year. General human access to the south-western corner, where most breeding occurs, has been restricted since 1986, and since 1996, this area has been closed to general access from November to April inclusive. Light-mantled sooty albatrosses are widely distributed around Macquarie Island, nesting mostly on the coastal slopes, and it is estimated that 1100-1500 pairs breed each year (T. Disney unpublished data in Gales 1998).

Wandering albatrosses are the largest of the four species and typically show a biennial breeding pattern when successful (Croxall 1991). Grey-headed albatrosses also tend to breed every second year when successful while Black-browed albatrosses generally follow an annual breeding pattern regardless of the outcome of the previous breeding attempt (Weimerskirch *et al.* 1986; Jouventin and Weimerskirch 1988; Croxall 1991). Light-mantled sooty albatrosses also typically defer breeding for at least one season after a successful breeding attempt (Jouventin and Weimerskirch 1988).

The timing of the breeding cycle also differs between species; Black-browed albatrosses lay from late September to the end of October and chicks fledge in late March and April while Grey-headed albatrosses generally lay through October and chicks fledge in April and May. Light-mantled sooty albatrosses lay in late October through to early November and chicks fledge through May and early June. The larger Wandering albatrosses have a significantly longer breeding cycle with eggs laid in December and chicks fledging in November or December of the following year (Figure 1.3).

Figure 1.2
Breeding areas of albatrosses on Macquarie Island

Figure 1.3
Approximate range of lay, hatch and fledging dates for albatrosses on Macquarie Island



Aspects of albatross biology and ecology have been studied on Macquarie Island at varying degrees of intensity over the last thirty years (Carrick and Ingham 1970; Tomkins, 1984, Tomkins 1985a; Tomkins 1985b; Copson 1988, de la Mare and Kerry 1994; Weimerskirch and Robertson 1994). However, with the exception of de la Mare and Kerry (1994), few data exist on the long-term population trends, particularly over the last decade. Gales *et al.* (submitted) described population trends and breeding success from the first four years of the study and documented the pelagic distribution of the species breeding on Macquarie Island using records obtained at sea.

Due to the long lived nature of the birds, their delayed maturity and other aspects of their life history, long-term, longitudinal data are required to confidently calculate parameters such as survivorship and recruitment (Croxall 1998). Therefore, the current study began with a long-term, ongoing planned time-frame, and seven field seasons have now been completed. Data on breeding birds were also obtained from historical biological logbooks dating back 45 yrs (Wandering albatrosses) and 25 years (Black-browed and Grey-headed albatrosses). These data were used in conjunction with data from the current study assist in the completion of the aims stated below, particularly, in the calculation of survivorship and recruitment.

1.3 AIMS OF THE STUDY

A substantial dataset is required to comprehensively assess the conservation status of any population. Baseline information from long-term studies on breeding numbers and trends is essential for such an assessment, but data on breeding phenology, breeding performance and foraging ecology are also fundamental (Boggs 1992; Croxall 1998; Cooper 2000). This study describes the results obtained from the first seven seasons of an ongoing project run by Nature Conservation Branch, DPIWE Tasmania. The author has conducted fieldwork as part of this project for five of these seven seasons. Data on the population trends, breeding biology and foraging ecology of all four albatross species are presented. When possible, specific aspects were investigated for all four species in order to facilitate comparisons. However, due to the small size of the populations, and logistical and budgetary constraints this was not always possible. In this context the aims of the thesis are as follows.

1. Identify and quantify trends in breeding numbers and survivorship in the vulnerable albatross populations on Macquarie Island. Identify factors that may be responsible for these trends.

2. Describe aspects of the breeding ecology of albatrosses on Macquarie Island that could influence breeding numbers and breeding success, specifically:
    a. Breeding success and individual breeder quality
    b. Breeding frequency
    c. Attendance patterns

3. Identify the foraging ecology of Black-browed and Grey headed albatrosses and describe the implications that this has on the above.

4. Describe the chick provisioning regime of Light-mantled sooty albatross on Macquarie Island in order to provide more information on the foraging ecology of this species.

5. Use the above data to comprehensively describe the current population status of albatrosses on Macquarie Island and identify the threats that may impact upon these populations in the future.

1.4 ORGANISATION OF THESIS

This thesis has been organised in such a way that the above aims are addressed in a logical sequence and to facilitate publication of this material in the near future. However, similar field methodology was used to obtain data for several aspects of the study and in order to minimise repetition, a chapter outlining all aspects of the field methodology follows this General Introduction. The methodology used in processing and analysing the data is outlined in each relevant Chapter.

The remainder of the thesis has been broadly divided into three sections:

1. Population trends and survivorship,
2. Breeding biology,
3. Foraging ecology.

Section 1 contains a single chapter that identifies the population trends of all four albatross species and includes survivorship analyses for Wandering, Black-browed and Grey-headed albatrosses. Factors that may have influenced population trends or variation in survivorship are identified and discussed, particularly the relationship between long-line fishing effort and survivorship.

The second section on breeding biology is partitioned into three chapters. Firstly, trends in breeding success from 1994/95 to 2000/01 are described for each species and using these data, individual breeders are assigned a quality index that quantitatively describes their ability to breed successfully. Factors that may have impacted on breeding success are also discussed. Secondly, the breeding frequency of the four species is described, both for the breeding populations as a whole and also in the context of individual breeder quality. The relationship between partner fidelity, location changes, timing of failures and breeding frequency is also analysed. The third chapter of the breeding biology section describes the attendance patterns of the four species on Macquarie Island and some of the more basic breeding biology parameters are also documented here. Again, this is examined in the context of the entire breeding population (or a significant sub-sample in the case of the Light-mantled sooty albatrosses) and in relation to individual breeder quality. The relationship between attendance patterns and breeding success is also examined.

The third section contains two chapters that clarify some aspects of the foraging ecology of Black-browed, Grey-headed and Light-mantled sooty albatrosses. A total of three Black-browed albatrosses and five Grey-headed albatrosses were satellite tracked during the late incubation and early brood guard stage and their foraging movements are analysed in relation to potential interactions with fisheries and the surrounding oceanography. The chick-provisioning regime of Light-mantled sooty albatrosses was monitored for two seasons, five chicks each season and these results are described in detail in the final chapter of the foraging ecology section.

An attempt was also made to investigate the foraging ecology of Wandering albatrosses as part of the current study using LOTEK archival geo-location tags. Unfortunately, despite successful deployment and retrieval of five tags, the battery connection broke loose in every tag soon after deployment, and therefore no meaningful data on the foraging ecology of this species were obtained.

The thesis concludes with a General Discussion that describes the current status of all four populations of albatross species on Macquarie Island. The links between the aspects of the study are described and their implications on future survival of these four species are interpreted. The major threats that are facing these populations are identified and potential mitigation measures are proposed. A brief synopsis of potentially useful future research on the albatrosses of Macquarie Island is also included.

Chapter 2 - General Field Methodology

2.1 INTRODUCTION

The Australian Antarctic Division (AAD) provided transport to and from Macquarie Island each field season and the timing of the fieldwork was determined by the shipping schedule. The timing of breeding of all albatross species also influenced the nature of the field methodology and the timing of these breeding cycles is outlined in Figure 1.3. Fieldwork needed to begin in late September or early October each year to comprehensively determine breeding numbers of Black-browed albatrosses. This was achieved for all but one season of the study to date (1999/00 - arrived early November). Breeding numbers were estimated in 1999/00 by identifying failed nests and failed breeding birds. To avoid this happening in the 2000/01 season, the author over wintered on Macquarie Island, which allowed an extension to the end of the 1999/00 season and a optimal starting time to fieldwork in the 2000/01 season.

The nature of the fieldwork also had to be compatible with the conservation status of the small breeding populations on Macquarie Island. These populations are particularly susceptible to disturbance due to their small size, and therefore research strategies that minimise disturbance were required. Consequently, most attendance data were obtained using daily observations, diet samples were only collected opportunistically, and the sample sizes used for satellite telemetry studies were minimal.

Niaznol dye was used to colour mark all species when necessary. This dye was made by dissolving Niaznol powder (α-phenylene diamine) in alcohol and water and adding Gum Arabic and sodium sulphite. This stock solution is then 'activated' by the addition of a small amount of hydrogen peroxide prior to application. This dye breaks down under UV light but generally lasts a summer season when a fresh mixture is used. The albatrosses showed significantly less reaction to this dye in comparisons to a variety of spray paints that were trialed in the first and second seasons of the current study. When marking birds a small amount of the dye was applied to the breast of the bird with a long handled paintbrush.

The general census methodology, identification of breeding birds and attendance methodology used in each of the seven seasons are presented here for each species in the same temporal order in which they lay. Separate descriptions of the deployment of the Platform Terminal Transmitters (PTTs) and automatic weighing nests are also included. The taxonomy used to describe species follows that described in Robertson and Nunn (1998).

2.2 GENERAL FIELD METHODOLOGY

2.2.1 Black-browed albatrosses

2.2.1.1 Study Site

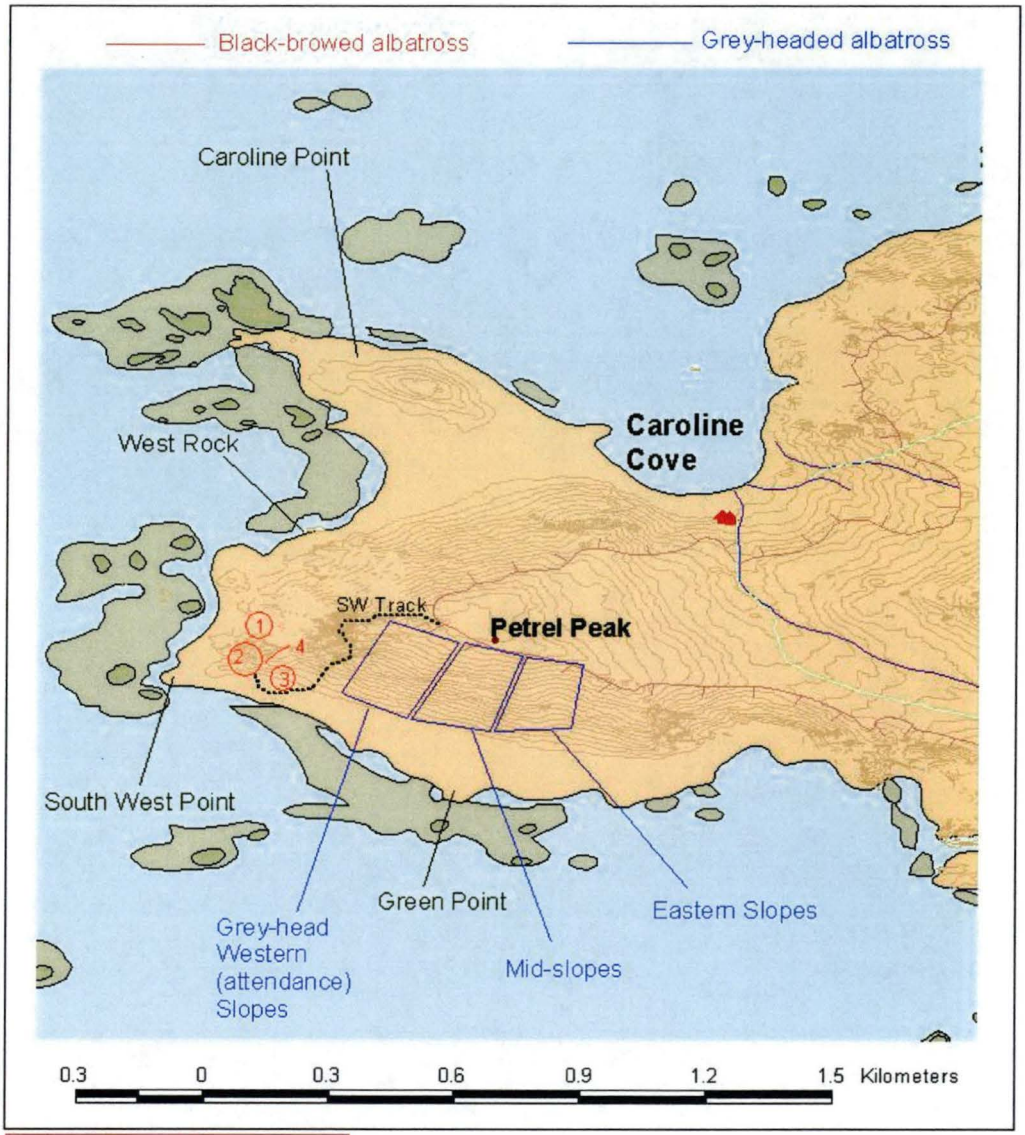
Black-browed albatrosses breed in seven localities (main colony, north tussocks, east tussocks and the ridge above, South West Point, West Rock, South West Track and the Grey-head albatross attendance slopes). These areas are geographically close to each other and all lie around the south western coast of Macquarie Island (See Figure 2.1). Nests were marked with individually numbered, short (~40 cm) length of orange electrical conduit. Most breeding nests were identified after the first week or two of daily observations and added to maps of each location.

2.2.1.2 Monitoring methodology and timing

Consistent methodology was used each year and daily observations usually began in late September/early October and continued until the end of October. The exception was the 1999/00 season when we arrived in mid-November and the number of breeding Black-browed albatrosses in this season was estimated by identifying failed nests and failed breeders, which were added to the number of incubating birds to estimate total breeding numbers.

Breeding birds were initially identified by their stainless steel or darvic bands during this time and attendance data during early incubation were also collected. Disturbance was kept to a minimum with nests usually only approached to read bands and colour mark birds. One visit was made to the colonies each day and the time of observations at the colony was recorded). When a new egg was observed, the bird on the egg was marked with Niaznol dye on the breast so each partner could be identified, and subsequently shift data were obtained by identifying the marked or unmarked bird on the nest each day.

Figure 2.1
Location of main breeding areas of Black-browed and Grey-headed albatrosses on Macquarie Island



Daily observations ceased for three to four weeks in November while breeding success sites for Light-mantled sooty albatrosses were set up around the island. One or two checks of the breeding Black-browed albatrosses were generally made during November so any failures in this time period could be identified. Daily observations re-commenced in late November/early December and continued until chicks were unattended in late January. Following the cessation of daily observations, regular checks were made until the chicks were banded in mid-March and the end of the season was determined by the timing of the last ship leaving Macquarie Island. After our departure, Tasmanian Parks and Wildlife (TASPAWS) Field Officers monitored the chicks every two to three weeks to obtain approximate chick fledging dates.

2.2.1.3 Checking bands and marking birds

In order to minimise disturbance to pre-laying birds, band numbers were usually only read after the egg was laid. The temperament of each bird was assessed and scored each time (scores from 1 - calm to 3 - agitated). These scores allowed the temperament of individual birds to be monitored over time and facilitated the identification of appropriate birds for satellite telemetry studies. The sex of each bird could only be conclusively established by observing copulation or egg-laying. In many cases there was a noticeable size difference in the head and bill, with males generally being larger than females, and the sex was also determined using these morphological differences when possible. Band numbers (stainless steel and darvic) were also checked opportunistically if non-breeding birds were present in the colony. Band numbers of non-breeding birds were also checked outside the colonies throughout the season at various locations around the slopes.

2.2.1.4 Banding adult/juvenile birds

Most breeding birds were banded with stainless steel bands in the first two seasons of the project. Birds were banded unrestrained on the egg or removed from the egg, restrained, banded, and replaced back on the nest. Unbanded non-breeders were banded opportunistically throughout each season with stainless steel bands and white darvic bands; however, pair bonding birds were not disturbed.

2.2.1.5 Chick banding

All Black-browed albatross chicks were banded in mid-March each season with stainless steel bands on the left leg and numbered darvic bands on the right leg. Colours were changed each year to facilitate the easy identification of different cohorts in future years. Three people were

involved in banding the chicks, one to restrain the bird, one to band and take measurements and one to record the data.

2.2.2 Grey-headed albatrosses

2.2.2.1 Study Site

The breeding population of Grey-headed albatrosses is confined to the slopes on the southern side of Petrel Peak, West Rock and the slopes opposite West Rock (Figure 2.1). Most bird's breed on the steep, tussocked (*Poa foliosa*) southern slopes of Petrel Peak that have been divided into three regions for monitoring purposes: the western (attendance) slopes, mid-slopes and eastern slopes (Figures 2.1, 2.2). Most breeding nests or potentially breeding nests were identified by mid-October each year and added to detailed maps of the slopes.

2.2.2.2 Monitoring methodology and timing

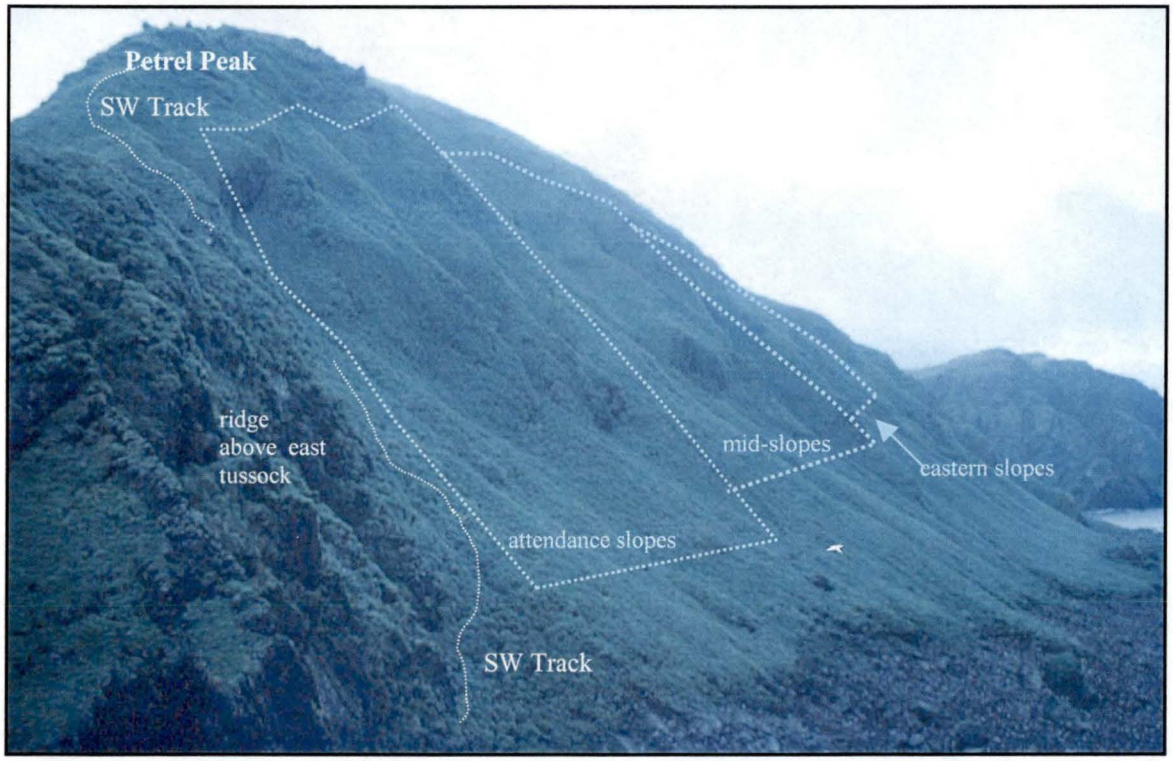
Observations of 'attendance nests' usually started in the first week of October and continued through to the beginning of November. Again, the exception was the 1999/00 season when observations began in November and the number of eggs laid was estimated by identifying failed nests and failed breeders. The observation regime of the attendance nests post November was the same as described for Black-browed albatrosses in Section 2.2.1.2.

Non-attendance sites were identified and mapped in the first two weeks in October. These nests were checked at least once a week whilst daily observations of the attendance nests were in progress. One or two checks of these nests were also made in November.

2.2.2.3 Checking bands and marking birds

Band numbers were checked after the egg was laid, just prior to marking the bird with Niaznol dye. In some cases the band number of birds occupying nests without eggs could be read unobtrusively using binoculars (Leica 8*20 BCA) and these were also recorded in the daily observations. Identification of the unmarked partner was obtained once incubation shifts commenced. The temperament of each bird was assessed each time and marking was not carried out if the bird was too wary.

Figure 2.2
Petrel Peak and southern slopes with approximate location of Grey-headed albatross study areas



Similarly to the Black-browed albatross, temperament scores were given to each bird that was approached. The sex of this species could only be conclusively established by observing copulation or egg-laying, as there was little morphological difference between male and female Grey-headed albatrosses. Band numbers of non-breeders, immature birds and possible failed breeders were also checked opportunistically during the daily traverse of the slopes. Immature or juvenile birds were identified by the presence of white feathers in the head and dark patches on the bill (Prince and Rodwell 1994).

2.2.2.4 Banding adult or juvenile birds

Similarly to the Black-browed albatrosses, most breeding Grey-headed albatrosses were banded in the first three seasons of the project. Most unbanded breeders were banded with stainless steel bands unrestrained on the egg or chick. Unbanded non-breeders were occasionally banded with stainless steel bands and white darvic bands if they were alone and were of an appropriate temperament.

2.2.2.5 Chick banding

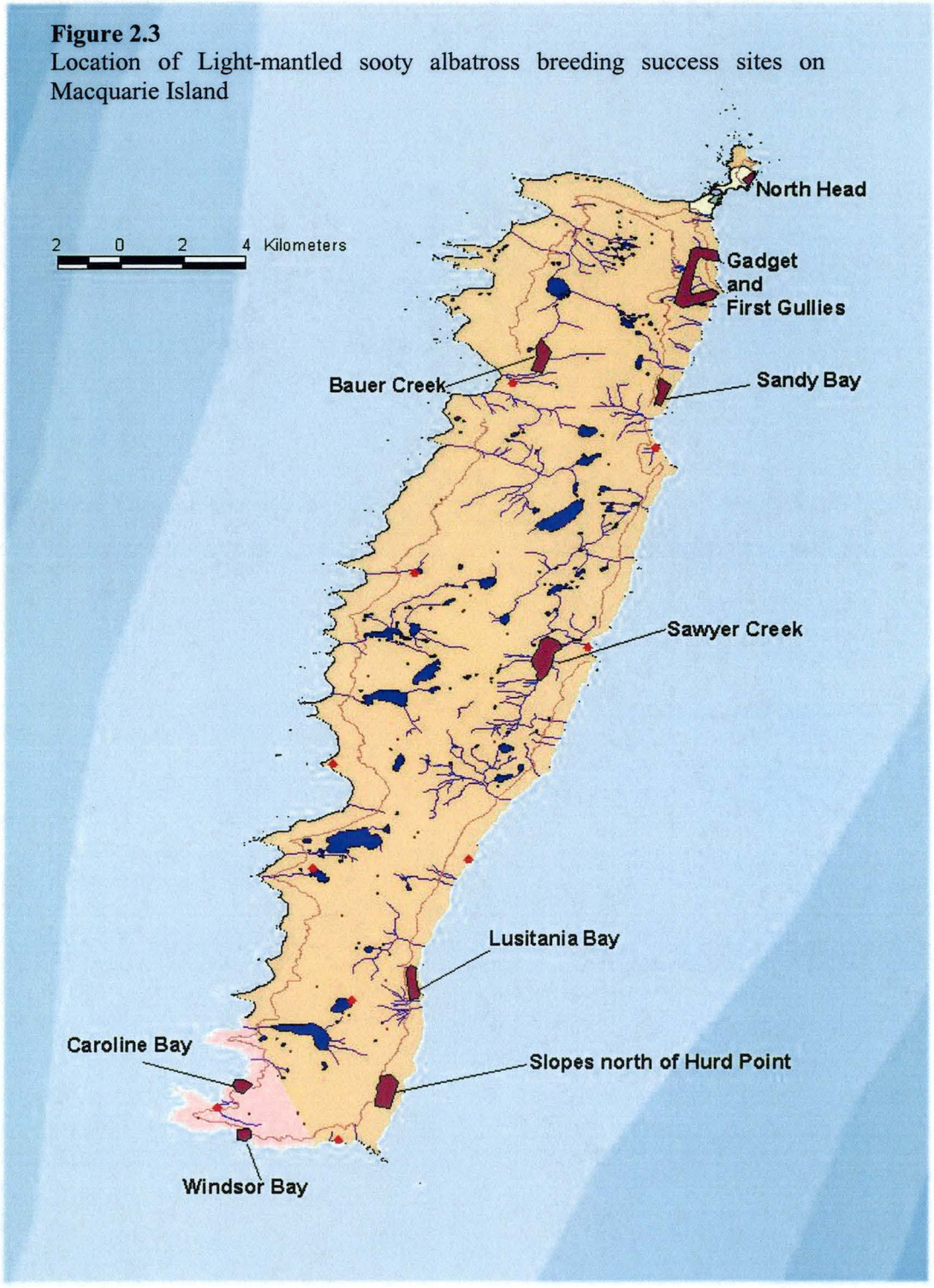
All Grey-headed albatross chicks were banded in mid-March each season with stainless steel bands on the left leg and numbered darvic bands on the right leg. Darvic bands with numbers that could be misinterpreted if read upside down (e.g. 066), were not used and colours were changed each year to facilitate the easy identification of different cohorts in future years.

2.2.3 Light-mantled sooty albatrosses

2.2.3.1 Study Sites

Due to the number of breeding birds and widespread nature of the breeding sites of Light-mantled sooty albatrosses it was not possible to monitor the whole population in a similar manner to the Black-browed and Grey-headed albatrosses. Six sites were set up in the first season of the project where breeding numbers were determined, breeding birds were banded and breeding success was calculated. Five of these sites were retained for the duration of the study and another three sites were added in 1995/96 and 1996/97. An additional inland site was added to the group in 1998/99 (Sawyer Creek). These nine sites formed the basis of the study into population numbers and breeding success of this species. The sites were chosen to reflect a range of habitats and included both coastal and non-coastal sites (Figure 2.3).

Figure 2.3
Location of Light-mantled sooty albatross breeding success sites on Macquarie Island



Sites ranged from one to two square kilometres in area and usually contained between 20 and 50 breeding birds each season. Breeding birds were monitored remotely at two sites in an effort to establish if disturbance influenced breeding numbers or breeding success.

2.2.3.2 Observation methods

The nine Light-mantled sooty albatross sites were classified as accessible (nests monitored on the ground) or inaccessible (more difficult to access areas where nests were monitored remotely using binoculars or telescope). Two of the nine sites were in the latter category and all the nests in these areas were observed using binoculars (Leica 8*20 BCA) or a telescope (Nikon Field Scope 20x-40x). Most nests in the other seven sites were accessible.

Light-mantled sooty study sites were established in the first three weeks of November each season. Most breeders had laid by 5 November so censusing sites at this time allowed most nests to be found and few early failures were identified. Breeding nests were identified and mapped. These sites were then visited every 12-21 days. During each check every nest was re-visited to establish whether it was successful and incubating birds were identified or banded. Once both birds of a pair had been identified each nest only had to be checked for success or failure during each monitoring visit.

All nests with incubating birds were marked with individually numbered 40 cm lengths of orange electrical conduit. The pegs were placed close to the nest but in a position where they would not interfere with landing of the birds or with nest maintenance activities.

2.2.3.3 Banding adults

Incubating adults were checked for bands and if they were unbanded an attempt was usually made to band them. Adults were banded unrestrained on the nest and to avoid any accidental damage to the egg it was often replaced temporarily with a wooden one. Non-breeding birds were occasionally banded opportunistically throughout the season with stainless steel bands and white darvic bands.

2.2.3.4 Chick banding

All chicks in the accessible breeding success sites were banded in late March each season. This was generally a three-person operation with one person restraining the chick, another banding the bird and another writing down the details. This minimised the time around each chick and reduced disturbance.

2.2.3.5 Attendance patterns

Due to the difficulty in integrating daily observations of Light-mantled sooty albatrosses with the daily observations of the Black-browed and Grey-headed albatrosses, most of the data on attendance patterns of this species were collected using an Automatic Tracking System (ATS) and Very High Frequency (VHF) transmitters. This allowed the presence or absence of a bird to be continuously logged over a four to six month period and in addition to the attendance data, also provided information on the foraging regime during chick provisioning.

An attendance-monitoring site was established within the slopes north of Hurd Point breeding success site in 1998/99 and monitoring of breeding birds continued at this location in 1999/00 (ATS) and 2000/01 (daily observations). An ATS site was also established at Windsor Bay in 2000/01 (see Figure 2.3 for location of sites). At both locations the methodology used was similar and prior to setting up, appropriate nests were identified that could be used with the ATS. All transmitters and the ATS system were thoroughly tested in field huts before being deployed into the field.

The ATS consisted of a VHF - DCCII receiver connected to a data logger. The ATS was housed in a waterproof box enclosed in a tent set up on the slopes (see Figures 2.4 and 2.5). One or two 60 or 80-amp hour gel cell batteries were used to power the system and these were charged continuously by a wind generator. During periods of prolonged calm a petrol generator was taken to the site to charge the batteries. The transmitters were detected by a directional antennae attached to the receiver in 1998/99 and an omni-directional antennae was used in 1999/00 and 2000/01. The directional antenna detected transmitters up to 150 metres away within an arc of 50 degrees from the antennae. The omni-directional antenna used in the latter two seasons had a similar range and detected birds in a 360° arc around the antennae. This allowed more breeding birds to be included in the study of attendance patterns (and chick provisioning). After the ATS, receiver, logger and aerial had been installed we confirmed that the nests were all within the range of the antennae by testing transmitters at each nest site.

At the Hurd Point site the first group of ATS transmitters were attached to birds on eggs between 20 November and 1 December; transmitters were then attached to partners at the earliest opportunity. All transmitters were attached in late December or early January at the Windsor Bay site. Birds were not restrained and all transmitters were attached in a one-person operation.

Figure 2.4
ATS site at slopes north of Hurd Point (looking south) in 1998/99

Figure 2.5

ATS site at slopes north of Hurd point (looking east) in 1999/00

Transmitters were attached using Velcro bands sewed and cable tied onto the transmitters. Five-minute Araldite was also used when the transmitters were attached to the birds to ensure that that integrity of the Velcro was maintained. Transmitters were supplied by Sirtrack (Havelock North, New Zealand), each with a unique frequency between 150 and 151 MHz and were potted in epoxy impregnated with Kevlar. Each transmitter had a battery life of approximately five to six months and a pulse rate of 40 pulses per minute. The weight of the transmitters with the Velcro bands ranged from 7.6-7.8 grams. Figure 2.6 shows a sketch of the transmitter with dimensions and Figure 2.7 shows a unit attached to the leg of a Light-mantled sooty albatross in situ.

The receiver and logger were set up to scan continuously for the 16-18 frequencies and log the presence of each transmitter every 30 minutes. It is unlikely that any returning birds were missed using this sampling regime as it only took three to four minutes to scan all 16-18 frequencies. Data were downloaded from the logger fortnightly and processed. One bird from each of the nine pairs was marked with Niaznol dye and every time the site was checked (daily until the end of December, and at least weekly after that) the presence of the marked or unmarked bird was recorded. These data were used to check that transmitters were working and the ATS was functioning properly. One or two breeders did not have transmitters attached each year due to their aggressive or wary temperament. The ATS gear was removed in late March of the 1998/99 and 2000/01 field seasons, but was left in until chicks fledged (June 2000) in season 1999/00.

The site at the slopes north of Hurd Point was monitored daily during late October 2000 (pre-breeding) and throughout early incubation in an effort to maximise the chance of retrieving VHF transmitters that were deployed in 1998/99 and 1999/00.

2.2.4 Wandering albatrosses

2.2.4.1 Study Site

Wandering albatrosses breed primarily in the south-western corner of Macquarie Island around Petrel Peak and the Caroline Cove amphitheatre; however, a small number also breed each year on the north-western featherbed (Figure 1.2). Daily observations of breeding and non-breeding birds were restricted to the south-western area; however, pair identities and approximate laying and hatching dates were generally obtained for breeders in the northern area. The south-western area was divided into 13 sub-regions, which allowed the location of breeding and non-breeding birds to be described more accurately (Figure 2.8)

Figure 2.6
VHF transmitter: design and dimensions (weight =7.7g)

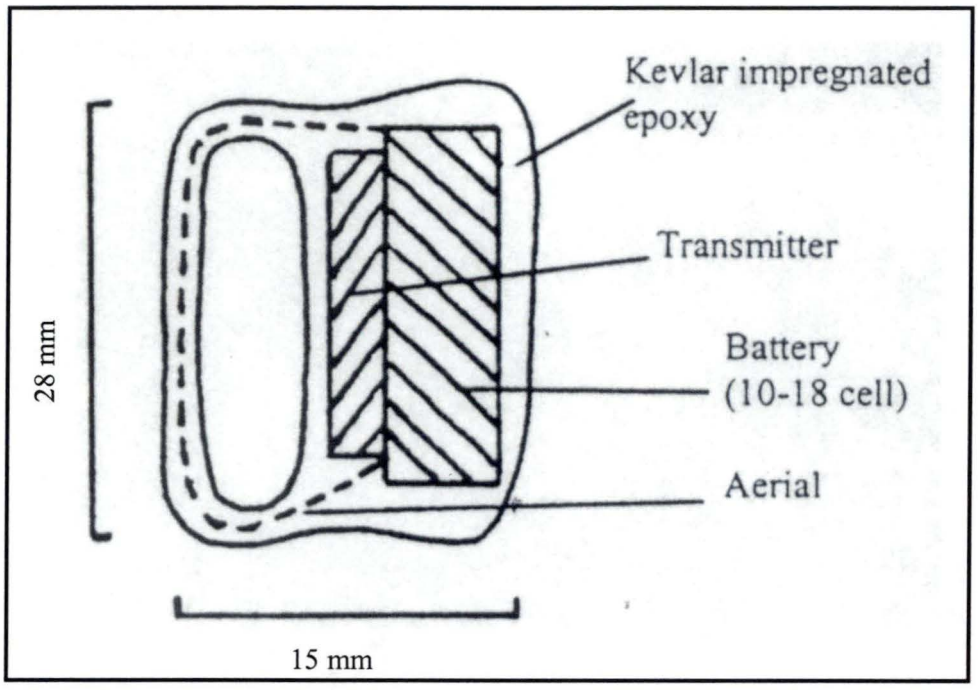


Figure 2.7
VHF transmitter attached to the leg of a Light-mantled sooty albatross

2.2.4.2 Monitoring methodology and timing

Daily observations of breeding or potential breeding birds around the Caroline Cove commenced in late November of each field season and continued until our departure at the end of the season. Some opportunistic observations of returning birds were made prior to this in early November during brief trips to the Caroline Cove area.

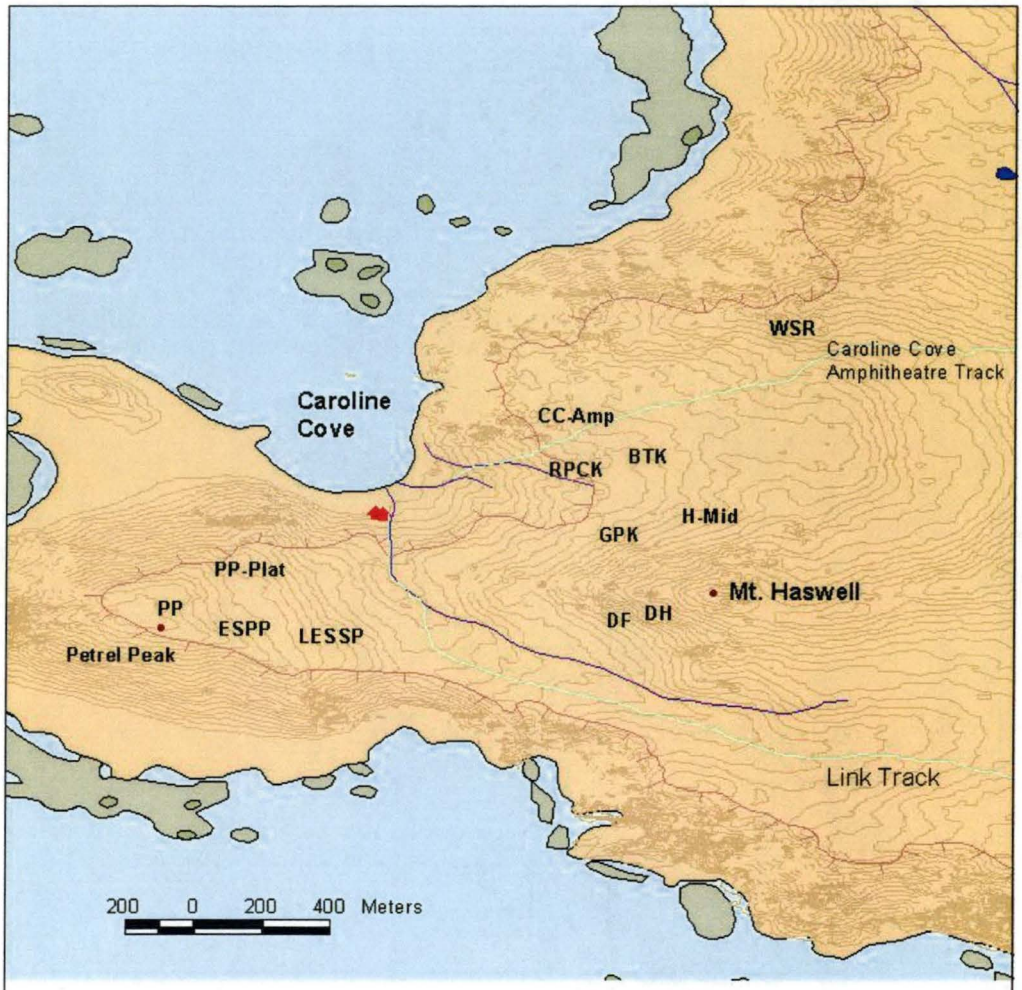
Potential breeding pairs were identified throughout December, and nests were mapped onto sketch maps similar to Figure 2.8. Nest markers were used in the first four seasons to mark out breeding nests but in the following three seasons accurate mapping was sufficient to find and locate nests. Daily trips were made up Petrel Peak and through the Caroline Cove amphitheatre to monitor the progress of the breeding birds and ascertain laying and hatching dates. Once the egg had been laid the bird on the egg was identified and the partner was identified after the first changeover. Most breeding birds could be sexed by plumage differences and the presence of the male or female was noted each day for attendance purposes.

Non-breeders in the areas were also identified when possible. Nests with breeding birds were rarely approached closely and disturbance of the breeding birds was kept to an absolute minimum. Non-breeders were also not disturbed if they were interacting with other birds.

2.2.4.3 Banding

Many Wandering albatrosses had been banded before the project began with Monel or stainless steel bands and some birds also had different combinations of coloured plastic bands. Unbanded breeders, non-breeders and chicks were banded with Monel or stainless steel bands and white numbered darvic bands as part of the current study. Breeders were banded unrestrained on the nest while non-breeders and chicks were restrained and banded. Non-breeders were only banded if the bird was not interacting with any other birds.

Figure 2.8
Location of areas used to describe locations of breeding and non-breeding Wandering albatrosses on Macquarie Island (1994/95 –2000/01)



Key

PP - Petrel Peak
ESPP - Eastern shoulder Petrel Peak
LESPP - Lower eastern shoulder Petrel Peak
PP-Plat - Petrel Peak mid plateau
DF - Display Flat
DH - Display Hill
GPK - Giant Petrel Knoll
H-mid - Mt. Haswell mid-tongue
RPCK - Royal Penguin colony knoll
BTK - Bare topped knoll
CC-Amp - Caroline Cove amphitheatre
WSR - West Sodomy Ridge

2.2.5 Satellite tracking – Field deployment of PTTs (Chapter 7)

2.2.5.1 Overview

In seasons 1999/00 and 2000/01 five Grey-headed albatrosses and three Black-browed albatrosses were tracked using the ARGOS satellite telemetry system and Microwave Telemetry PTTs (Table 2.1). Black-browed albatrosses were conclusively sexed by observing copulation while Grey-headed albatrosses were sexed by identifying the bird on the nest directly after the egg was laid. The sex of birds tracked and the number of foraging trips recorded are summarised in Table 2.1.

Table 2.1
Summary of satellite tracking deployment details during 1999/00 and 2000/01

Species / season	Sex			PTT deployment		Foraging trips		Tracked foraging duration (days)
	m	f	un	Attached	Removed	Inc.	Brood-guard	
Black-browed albatross								
1999/00	0	1	0	20/12/99	20/1/00	1 long	6 short	18.7
2000/01	1	1	0	28/11/00	25-27/12/00	3 long, 4 short	-	27.5
Grey-headed albatross								
1999/00	1	2	0	20/12/99	15-19/1/00	2 long	3 long, 4 short	44.4
2000/01	0	1	1	28/11/00	lost at sea 15-25/12/00	2 long	1 short	18.6

The PTTs weighed thirty grams and were approximately 50 mm long, 15 mm high and 15 mm wide (Figures 2.9). The PTTs had a battery life of approximately 700 hours, were configured to run continuously and pulsed at 90 pulses per minute during their deployment. In each case the units were attached prior to chick hatching to collect information on late incubation shifts and brood/guard shifts.

2.2.5.2 Attachment of units

In each case the units were tested to ensure that they were working before they were attached to the birds. Four units were attached on 20 December 1999 and another four on 28 November 2000. The birds were removed from their egg, restrained and the units attached to feathers on the back with the anterior end of the unit near the base of the neck (i.e. antennae furthest away from neck – Figure 2.10). The units were attached to three small groups of feathers close to the skin with three wraps of Tesa© tape, one wrap encircling each group of feathers and the PTT and finishing off the wrap by sticking the tape to itself. Small pieces of Tesa© tape (approximately 3cm long) were then used to tape the join of the three wraps to ensure that they could not easily be preened loose. The bird was then released back onto the nest and settled on the egg soon after. Once attached, the units settled against the back of the bird underneath most of the feather with only the antennae protruding (Figure 2.10).

2.2.5.3 Retrieval

Retrieval times and the dates that the two PTTs were lost are contained in Table 2.1. When the remaining units were retrieved, a scalpel blade was used to slice through the Tesa© tape wraps and the PTT removed. Following this, the rest of the tape was removed from the feathers. The birds were not restrained during the removal of the units.

2.2.5.4 Selection of birds

Each bird used in this study was carefully chosen for its temperament and pair/nest bond. Records from earlier seasons were used to evaluate the breeders that were most likely to cope with being removed from the nest, restrained then returned to the nest. This selection process played an important part in the success of the operation and it is unlikely that just any breeding bird of both species could be subjected to this treatment without deserting the nest.

Figure 2.9
Microwave Telemetry Platform Terminal Transmitter (30g_PTT_100)

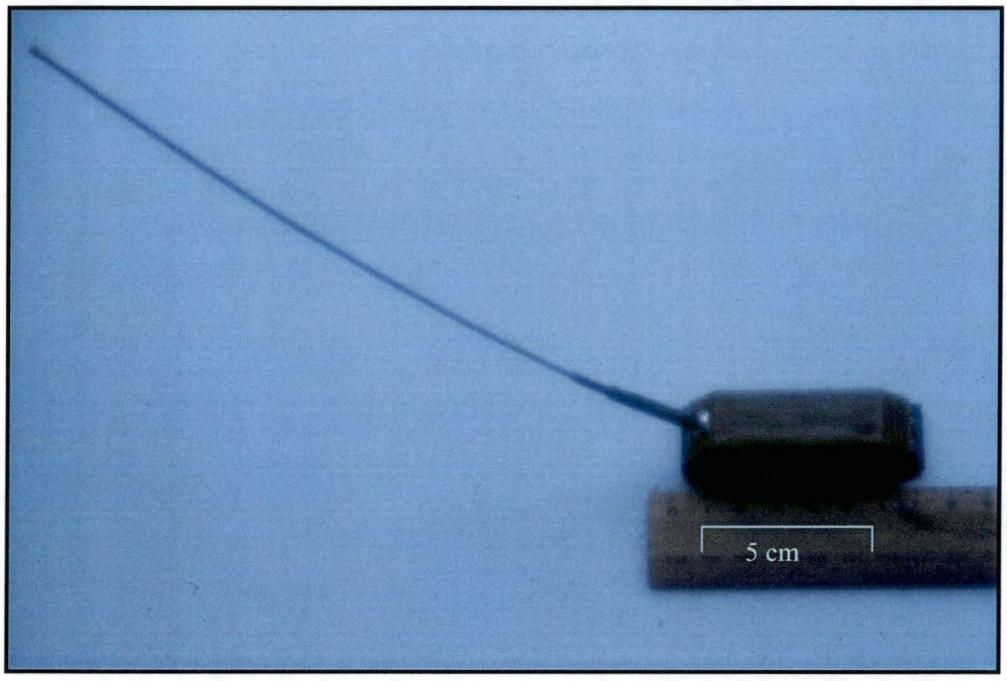
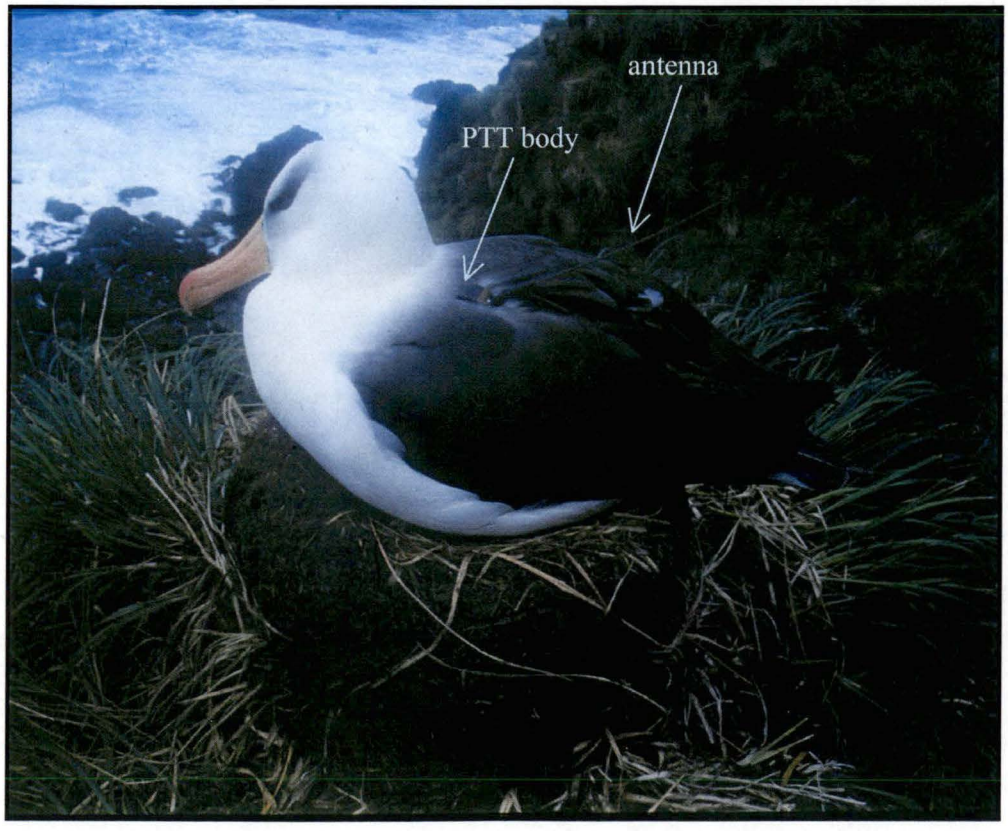


Figure 2.10
Black-browed albatross with PTT attached, Petrel Peak, December 1999



2.2.6 Chick provisioning (Chapter 8)

2.2.6.1 Overview

Five automatic weighing nests (Francis Scientific Instruments, Cambridge, UK) were installed underneath Light-mantled sooty albatross chicks for the first time in January 2000, and these nests were again deployed at the Windsor Bay site in January 2001. The nests used consisted of a fibreglass bowl and base that housed the weighing platform (Figure 2.11) and were powered by eight AA batteries housed in the datalogger that was connected to the nest by a 5m power cord. The nests were tested and calibrated in field huts then tested again out in the field during installation with known weights. Chick masses were subsequently recorded (±10g) every ten minutes and data were downloaded from the data-loggers with a laptop computer at three to nine day intervals.

2.2.6.2 Study sites and installation

The nests were installed between the 24 and 28 January in both 2000 and 2001, two to five days after the chick was left unattended for the first time. As the chick provisioning study was run in conjunction with the ATS, the automatic weighing nests were installed at the slopes north of Hurd Point breeding success site in 1999/00. In order to increase the sample size for the attendance study and access sufficient numbers of breeding birds, a new site at Windsor Bay, approximately four kilometres to the west of the 1999/00 site, was used in 2000/01.

The chicks were removed from the original nest and placed in an unoccupied nest nearby. The automatic weighing nest was then installed in exactly the same location as the original nest, levelled and calibrated. The chick was then placed into the automatic weighing nest where it settled immediately. In most cases nests were selected where both parents had a VHF transmitter attached. The nests were calibrated again approximately five weeks after they were installed and when they were removed. There was no significant variation in the new calibration constants compared to the calibration constants that were originally calculated.

2.2.6.3 Removal of automatic weighing nests

The nests were removed in late May 2000 in the 1999/00 season after the chicks had fledged. In a few cases the chicks left and returned to the nest as fledging approached. Nests were removed in late March in the 2000/01 field season. In the latter season, chicks were removed from the automatic weighing nests, placed into an unoccupied nest nearby and the original

nest was replaced on the original nest site. The chicks were then placed back into their original nests and again, settled quickly once we had departed the area.

Figure 2.11
Light-mantled sooty albatross chick close to fledging on an automatic weighing nest at the slopes north of Hurd Point.

2.2.7 Data obtained and relevance to each chapter

Establishing how many eggs were laid each year was fundamental to the data collection and allowed population trends (Chapter 3) and breeding success (Chapter 4) to be determined. Identifying breeding pairs each year was integral to the analysis of breeding frequency and associated aspects such as partner fidelity (Chapter 5). The resight data of both breeding and non-breeding birds were also utilised in the survivorship and recruitment analyses (Chapter

3). Daily observations (Black-browed, Grey-headed and Wandering albatrosses) provided detailed information on attendance patterns during early incubation, late incubation and the brood guard stage of the Light-mantled sooty albatross breeding cycle (Chapter 6). These daily observations also formed the basis of the investigation into breeding success, and in conjunction with the identification of breeding birds, was used to ascertain the 'breeding quality' of individuals (Chapter 4). Banding all chicks each year was important for the ongoing investigation into survivorship and recruitment.

The ATS provided detailed information on attendance patterns during late incubation and the brood guard stage of the breeding cycle (Chapter 6). The ATS system was also integral to the chick provisioning study (see Methods 2.2.5 and Chapter 8). Data from the fortnightly monitoring checks of the Light-mantled sooty albatross study sites were used in the investigation into breeding success, and in conjunction with the identification of breeding birds, also used to ascertain the 'breeding quality' of individuals (Chapter 4).

Chapter 3 - Population trends and survivorship of albatrosses breeding on Macquarie Island.

3.1 INTRODUCTION

Many albatross populations around the world have been declining over the last three decades and most have been associated with interactions of albatrosses with long-line fisheries (Gales 1998). The numbers of hooks set, the spatial locations of the operations, the type of long-lining and the mitigation methods utilised have varied significantly over this time period (Brothers 1991; Murray *et al.* 1993; Ashford *et al.* 1996; Brothers *et al.* 1999; Gales *et al.* 1999; Ryan and Boix Hinzen 1999). Consequently albatrosses have been exposed to varying degrees of threat and populations have often fluctuated in response (Weimerskirch and Jouventin 1987; Croxall *et al.* 1990; de la Mare and Kerry 1994; Prince *et al.* 1994; Croxall *et al.* 1998; Weimerskirch *et al.* 1998; Walker and Elliott 1999; Waugh *et al.* 1999b; Inchausti and Weimerskirch 2001; Nel *et al.* 2002a). The characteristic and extreme life history attributes of albatrosses make them particularly vulnerable to any elevated levels of mortality. Consequently long-term population studies are required to ascertain trends in population numbers.

Long-line fishing is banned within the Macquarie Island Economic Exclusion Zone (EEZ) (200 nautical miles circle centred on Macquarie Island) and in the absence of illegal fisheries, the threat to birds from this type of fishery in the immediate vicinity of Macquarie Island is low. However, it is possible that illegal long-line fishing vessels do operate within this zone, and the impacts of the trawl fishery for Patagonian Toothfish (*Dissostichus eleginoides)* that currently operates around Macquarie Island are still being assessed (Chapters 4 and 7). All four species forage in distant oceanic waters at some stage of the breeding cycle (Chapter 6, Chapter 7) and all are known to be caught and killed in Southern Hemisphere long-line fisheries for tuna, including those operating in Australian (Brothers 1991; Klaer *et al.* 1995; Klaer and Polacheck 1997; Gales *et al.* 1999) and New Zealand waters (Murray *et al.* 1993).

The small size of the breeding populations of Wandering (*Diomedea exulans*), Black-browed (*Thalassarche melanophrys*) and Grey-headed albatrosses (*Thalassarche chrysostoma*) on Macquarie Island make them particularly vulnerable to elevated levels of mortality. Between seven and twelve pairs of the biennially breeding Wandering albatross nest each year on Macquarie Island and the current breeding population is estimated at 19 breeding pairs. Three small colonies of Black-browed albatrosses and several individually nesting pairs breed

annually on Macquarie Island, constituting a breeding population of 38-45 pairs each year (Gales *et al.* in press). Over 100 pairs of Black-browed albatrosses breed on the Bishop and Clerk islets 37 kilometres to the south of Macquarie Island and it was estimated in 1992 that the annual breeding population on these islets was approximately 140 pairs (N. Brothers, unpublished data). The annual breeding population of Grey-headed albatrosses on Macquarie Island is approximately 60-85 breeding pairs and is confined to a small, relatively inaccessible area on the southern slopes of Petrel Peak. Light-mantled sooty albatrosses are more common and it has been estimated that 1100-1200 pairs breed around the coast of Macquarie Island each year (T. Disney, unpublished data in Gales 1993). The latter two species breed every second or third year when successful.

The small breeding population of Wandering albatrosses on Macquarie Island has been studied intermittently since the 1950's but there are relatively few published data on population numbers or trends (e.g. Carrick and Ingham 1970; Tomkins 1985b; de la Mare and Kerry 1994). The breeding population of Wandering albatrosses has declined since the 1960's reaching a low of only two breeding pairs in 1984/85 and gradually increasing again through the late 1980's (Carrick and Ingham 1970; de la Mare and Kerry 1994). There have been no long-term studies of non-breeding Wandering albatrosses on Macquarie Island. During the summers of 1976 and 1977 observations on the attendance and behaviour of breeding and non-breeding Wandering albatrosses were conducted at Caroline Cove (Tompkins 1985a; Tomkins 1985b). No further studies were done until the beginning of the current study in 1994-95 when observations of non-breeder behaviour (primarily courtship behaviour) were conducted and potential pair bonds were predicted. These observations and quantification of non-breeder numbers each season form the basis of the study into the non-breeding population on Macquarie Island.

Studies on the population trends and/or survivorship of other albatross species on Macquarie Island are also rare. Copson (1988) represents the only published account of breeding numbers and success of Black-browed and Grey-headed albatrosses and this study was carried out between 1977 and 1985. However, there are relatively comprehensive banding records of these two species spanning the last 25 years and these were collated with data collected from the current study into a comprehensive database of banding and resight data. Unfortunately, in contrast to the Wandering albatross database, these data were not sufficiently detailed to allow annual breeding numbers to be ascertained before the start of the current study. However, these data were used to compile records of the number of chicks banded each year and resight data were also collated and used to calculate long-term adult survivorship and juvenile

recruitment of both species. All chicks from both species were banded each year as part of the present study to facilitate the comprehensive assessment of juvenile recruitment in the future.

There are no published accounts of population trends and numbers of Light-mantled sooty albatrosses on Macquarie Island, and although there is a large amount of historical information, little of it has been published and banding records are too patchy (both spatially and temporally) to use in survivorship and recruitment analyses. A one-year pilot study into the number of Light-mantled sooty albatrosses breeding on Macquarie Island was carried out in 1993/94, however, none of these data have been published to date. The paucity of reliable long-term data and the lack of knowledge on population trends combined with the risks these populations face from long-line fisheries led to the following research questions.

3.1.2 Summary of research questions

1. What are the trends in breeding numbers of the four albatross species on Macquarie Island over the time frame for which there are adequate data ?

2. Has adult survivorship and juvenile recruitment varied over the time frames for which there is adequate data ?

3. Is there any evidence that increased mortality due to long-line fisheries has influenced these trends ?

4. Are these trends consistent with those observed at other subantarctic study sites ?

3.2 DATA PROCESSING AND ANALYSES

3.2.1 Trends in breeding numbers

Breeding numbers of Wandering albatross between 1963 and 1993 were determined from data contained in biological notebooks archived by the Australian Antarctic Division and these numbers were also partitioned into northern and southern eggs with the dividing line approximately half-way down Macquarie Island. Comprehensive data on breeding numbers of Black-browed and Grey-headed albatrosses prior to the present study were sparse; however, data on the numbers of chicks banded each year were more common and were used to give provide some indication of historical breeding numbers. Resights of adult and juvenile Black-browed and Grey-headed albatrosses from the 1970's to the early 1990's were also obtained from the historical logbooks. These data, collected opportunistically, complemented data

collected as part of the current, more focused study and allowed long-term-trends to be assessed.

The methodology used to gather breeding effort data on both breeding and non-breeding Wandering albatrosses between 1994 and 2001 is described in Chapter 2, Section 2.2.4. The methodologies used to gather data on breeding Black-browed, Grey-headed and Light-mantled sooty albatrosses during the current study are contained in Chapter 2, Sections 2.2.1, 2.2.2 and 2.2.3 respectively. Data were collected on the entire breeding populations of Wandering, Black-browed and Grey-headed albatrosses, and a representative sub-sample of breeding Light-mantled sooty albatrosses was monitored in this investigation.

3.2.2 Survivorship analyses

3.2.2.1 Raw data

The databases consisting of the Wandering, Black-browed and Grey-headed albatross banding and resight data were each sub-divided into two databases; one containing banding and resight data of birds banded as chicks, and the other containing banding and resight data from birds banded as adults or juveniles (six databases in total). Each database was then were recoded in a binary format with a one representing a resight in a particular year and a zero representing no resight (hereafter referred to as encounter histories). These data were then imported into a text editor and saved as an .INP file, a type of text file that was used as the basis of analyses using the capture –mark recapture software.

3.2.2.2 Mark-recapture software

The encounter histories were used with mark and recapture survival rate estimation software (MARK 2.1 – Gary C. White, Colorado State University) to test a variety of models and estimate survivorship rates (Φ) and recapture probabilities (p). MARK 2.1 computes these parameter estimates via numerical maximum likelihood techniques (White and Burnham 1999). Models were ranked using Akaike's Information Criterion (AICc) (Akaike 1973) and the models with the lowest AICc were considered to be the most parsimonious. Parsimony in this context represents a trade-off between too few parameters and too little model structure (thus inducing model bias and underestimates of sampling variation), versus too many parameters and too much model structure (therefore inducing parameter estimates that lack precision and possibly inferring the existence of spurious effects) (Burnham and Anderson 1998)

Thus AICc values were used to select the model that best explained the variation in the data while using the fewest parameters. This method of model selection is useful as it works well when data generally meet standard mark-recapture assumptions (see below) and may perform better when these assumptions are violated (Burnham *et al.* 1995; Burnham and Anderson 1998). AICc values are also independent of the number of 'significance tests' performed (in contrast to Likelihood Ratio Tests) and therefore are not susceptible to significant results obtained by chance (Anderson *et al.* 1994). However, there is still some debate about the use of AICc model selection versus the traditional use of Likelihood Ratio Tests (LRT) (e.g. see review in Lebretton *et al.* 1992). Therefore, Likelihood Ratio Tests were also conducted between all nested models (models which were subsets of each other). This also allowed the assessment of time-dependent (and in some cases age-dependent) variation in the parameter estimates.

3.2.2.3 Models utilised

The models were based on the basic Cormack-Jolly-Seber (CJR) model where marked animals are released alive into the population and resighted visually with little or no disturbance. These models allow the calculation of time-specific survival and re-capture probabilities. The evolution of the basic model CJR model is documented in (Cormack 1964; Jolly 1965; Seber 1965) and has the following underlying assumptions:

1. Every marked (banded) animal present in the population at time (i) has the same probability of recapture (p_i)
2. Every marked (banded) animal in the population immediately after the time (i) has the same probability of surviving to time (i+1).
3. Marks (bands) are not lost or missed
4. All samples are instantaneous, relative to the interval between occasion (i) and (i+1), and each release is made immediately after the sample.

These assumptions were tested using Goodness-of-Fit tests (GOF) of the most general model. These GOF tests utilised a parametric bootstrapping approach where simulated encounter histories were constructed (100 simulations in this case) and the deviance of these simulations is compared to the actual deviance of the model (effectively testing the heterogeneity of the data). If these GOF tests provided evidence that the model did not fit the data, the above assumptions were considered to be violated. Many studies have shown that survivorship varies considerably with age, the most significant difference being between juvenile and adult survivorship (Croxall *et al.* 1990; Weimerskirch *et al.* 1997a; Croxall *et al.* 1998;

Weimerskirch *et al.* 1998; Waugh *et al.* 1999b). Consequently, if the above assumptions were shown to be violated then age-dependent models were fitted to the datasets.

The age-dependent models were structured so that survivorship to the first resight was calculated independently of survivorship to all subsequent recaptures resights. Once fledged, albatrosses generally spend several years at sea before returning to land (Weimerskirch and Jouventin 1987; Prince *et al.* 1994; Waugh *et al.* 1999b) and therefore when the age dependent models were applied to the 'banded as chicks' datasets, fledgling survivorship **(defined as survivorship of the fledgling to its first resight back on land)** and adult survivorship were effectively calculated. A summary of the models tested on the datasets compiled from birds that were banded as chicks is contained in Table 3.1. Model nomenclature follows Lebretton *et al.* (1992).

Table 3.1
Models fitted to banded as chicks (BAC) datasets

Model	Description
Time specific	
Φ(.) p(.)	constant survivorship, constant recapture probability
Φ(.) p(t)	constant survivorship, time dependent recapture probability
Φ(t) p(.)	time dependent survivorship, constant recapture probability
Φ(t) p(t)	time dependent survivorship, time dependent recapture probability
Age-dependent and time specific	
Φ{fl(.) ad(.)} p(.)	constant fledgling surviorship, constant adult survivorship, constant re-capture probability
Φ{fl(t) ad(.)} p(.)	time dependent fledgling survivorship, constant adult survivorship, constant re-capture probility
Φ{(fl(t) ad(t)} p(.)	time dependent fledgling survivorship, time dependent adult survivorship, constant re-capture probility
Φ{fl(.) ad(t)} p(t)	constant fledgling surviorship, time-dependent adult survivorship, time dependent re-capture probability
Φ{fl(t) ad(.)} p(t)	time dependent fledgling surviorship, constant adult survivorship, time-dependent re-capture probability
Φ{(fl(t) ad(t)} p(t)	time dependent fledgling surviorship, time dependent adult survivorship, time-dependent re-capture probability

These models were less meaningful in terms of age-dependent survivorship when applied to the 'banded as adults' datasets, but were still useful in assessing any differences between survival to the first and subsequent recaptures. Similarly to the time-dependent modèls, GOF tests were also applied to the age-dependent models to test their fit to the data. Models that included both time dependent and age dependent parameters were also tested. Re-capture rates of Wandering and Grey-headed albatrosses were likely to be underestimated using the above models due to biennially breeding nature of these species when successful. Rothery and Prince (1990) showed that the first two years and the last year of a time series were the most biased estimates; however, these authors suggested that only estimates from the last year would be significant. Therefore estimates in the last year of the time-series were not used in the current study.

3.2.2.4 Long-line fisheries data

Long-line fisheries data were obtained from global databases (CSIRO – Marine Research, Hobart) that comprehensively documented spatial and temporal trends of tuna long-line fishing effort (Cathy Bulman - personal communication, Tuck and Bulman 2001). The data obtained (hooks set per year) were combined data from all fishing fleets and partitioned into different spatial areas (Figure 3.1, Table 3.2). These data were used to identify any relationships between the numbers of hooks set per year and trends in breeding numbers and/or survivorship.

Table 3.2

Spatial areas[1] for which annual numbers of hook set data[2] were obtained[3]

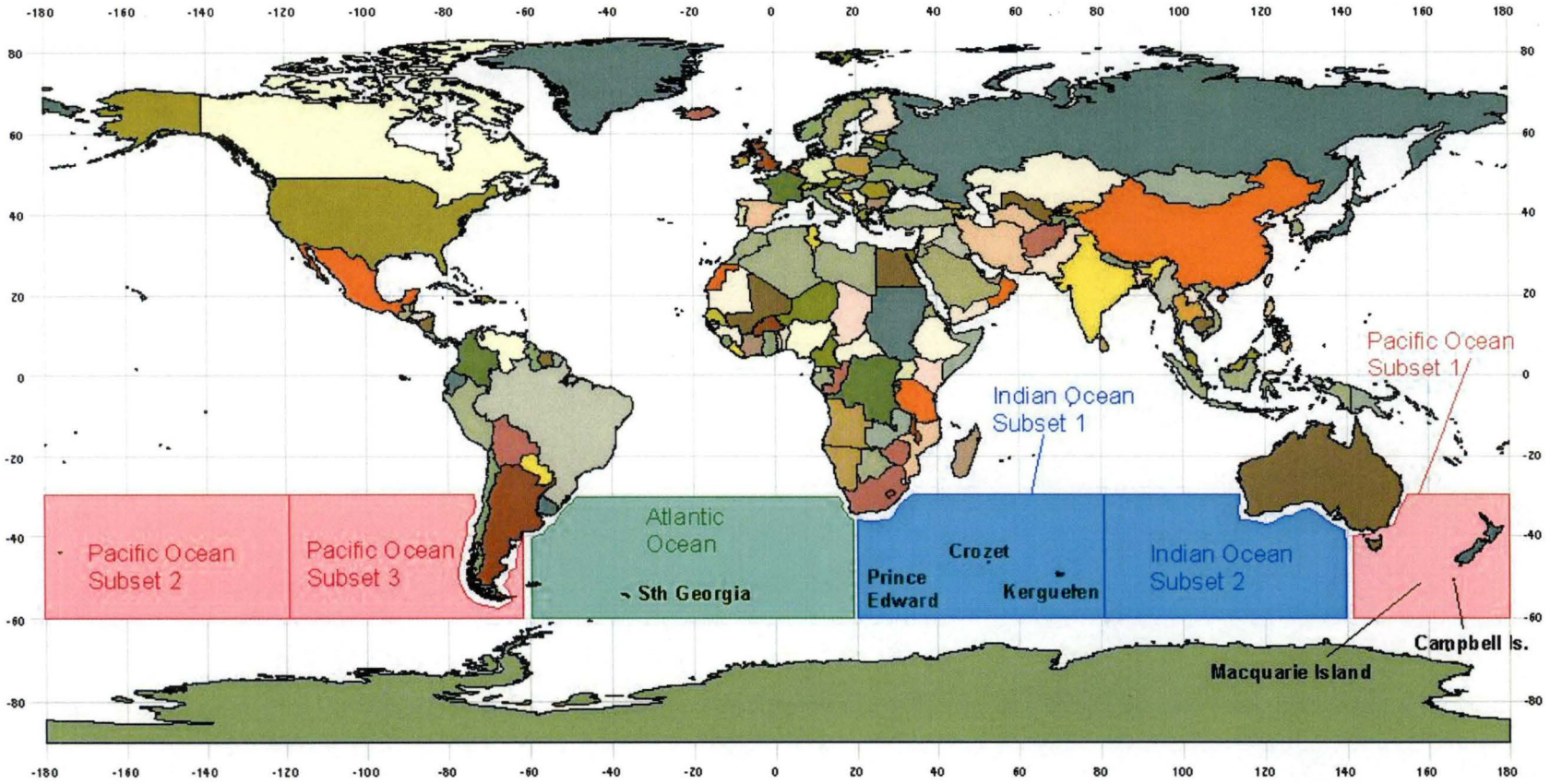
Area	longitude 1	longitude 2	time frame
Southern Hemisphere	0	360	1959-2000
Indian Ocean	20	140	1959-2000
Pacific Ocean	140	290	1962-2000
Atlantic Ocean	290	20	1960-1999
Indian Ocean subset 1	20	80	1959-2000
Indian Ocean subset 2	80	140	1959-2000
Pacific Ocean subset 1	140	180	1962-2000
Pacific Ocean subset 2	180	220	1962-2000
Pacific Ocean subset 3	220	290	1963-2000

[1] All data refers to effort between 30°S and 60°S

[2] Tuna long-lining only, does not include CCAMLR areas

[3] Source: Tuck and Bulman, 2001; Cathy Bulman, personal communication

Figure 3.1
Map of the world showing geographic areas for which fishing effort data were obtained



These data do not include illegal fishing effort (Tuck and Bulman 2001; Tuck *et al.* in prep), or long-line fishing for Patagonian Toothfish; however, in the context of the population trends under investigation, are considered to be a good starting point for these analyses.

3.3 RESULTS

3.3.1 Population Trends

3.3.1.1 Wandering albatrosses

3.3.1.1a Breeders

The number of Wandering albatrosses breeding on Macquarie Island has fluctuated considerably since the arrival of the sealers in the late 1800's. The discovery of over 100 Wandering albatross skulls in Aurora Cave suggest that numbers in the 19th century were significantly higher than the single breeding pair documented in 1911/12 (Carrick and Ingham 1970). Following the departure of the sealers, the Wandering albatross population slowly recovered until 1951 when there were at least 17 breeding pairs in total, and at its peak in the mid-1960's the total breeding population was estimated at 44 pairs (Carrick and Ingham 1970). The population then started to decline again in the late 1970's reaching another low point in the mid-1980's (less than five breeding pairs in total). Since then the population has gradually increased to its current level of approximately 19 breeding pairs (Figure 3.2).

Banding and resight data from 1960 to 1994, in conjunction with data from the current study, were used to compile a comprehensive picture of the variation in breeding numbers from 1963/64 to 2000/01 (Figure 3.2) The number of eggs laid in the north of the island was partitioned from the number of eggs laid in the south with the dividing line running east-west approximately half way down Macquarie Island. The breeding range of this species in the 1960's was considerably larger than it is today. During this time, breeding birds were found nesting on the 'featherbed' area throughout the west coast of Macquarie Island as well as the southern area.

Most of the decrease in the late 1960's and early 1970's could be attributed to a decrease in pairs breeding in the north and west of the island, whereas the further decrease in the late 1970's and early 1980's was attributable to a decrease in both the northern and southern breeding birds. The increase that has been observed in the last 15 years is largely attributable to an increase in southern pairs. The number of chicks that fledged from Macquarie Island since 1963 is illustrated in Figure 3.3.

Figure 3.2
Number of Wandering albatross eggs laid on Macquarie Island each year from 1963 - 2000

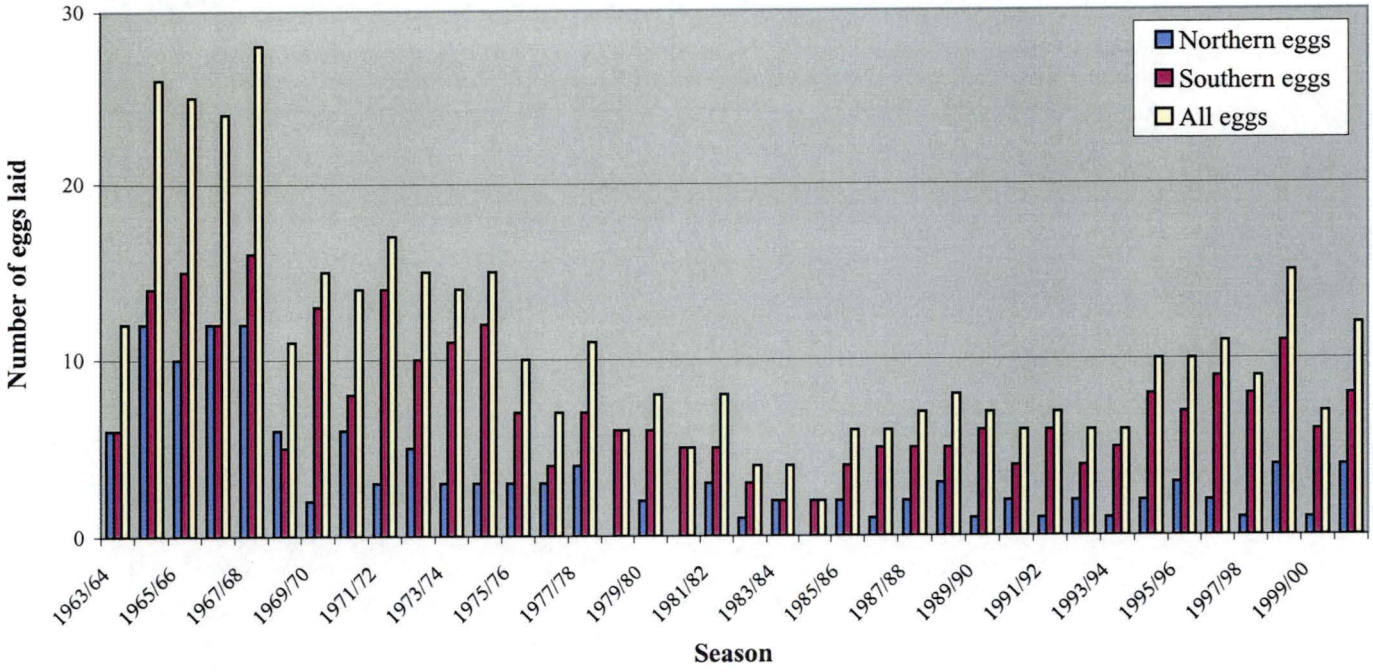
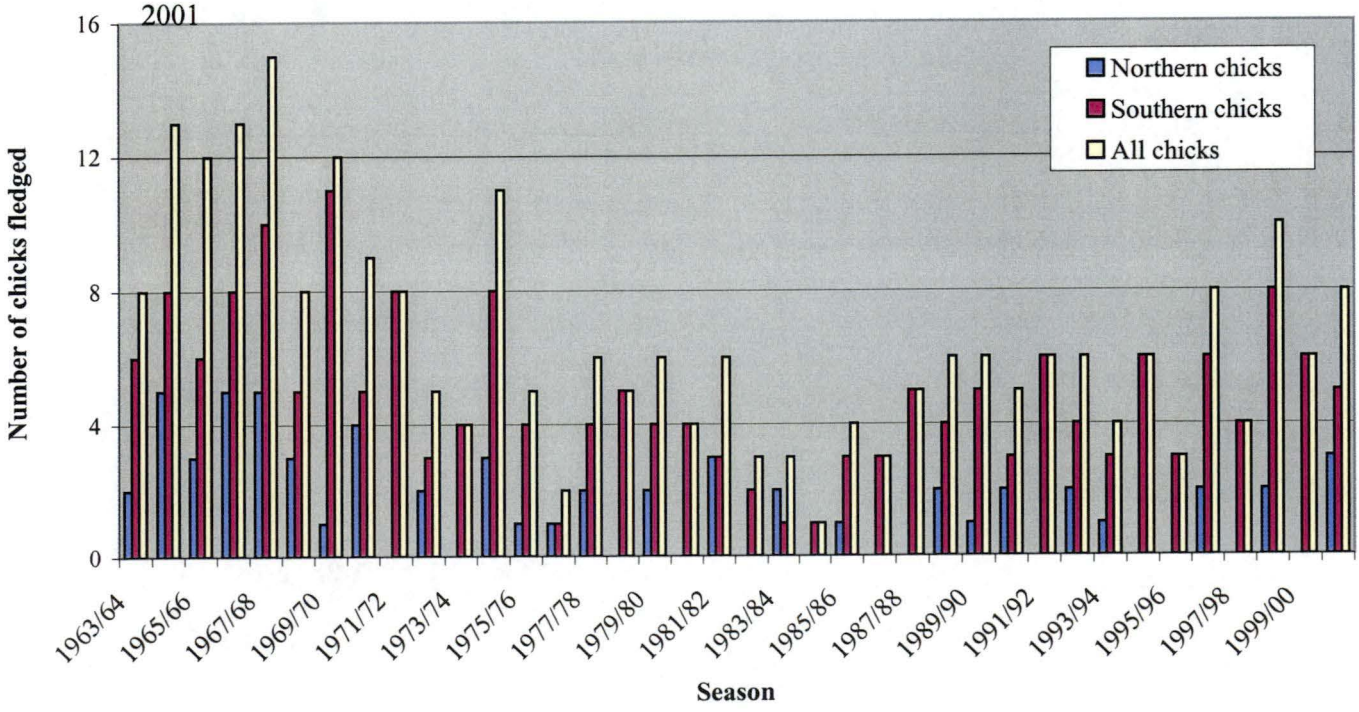


Figure 3.3
Number of Wandering albatross chicks fledged from Macquarie Island between 1964 and 2001



Although variation in breeding success precludes the use of this type of information as an absolute indication of breeding numbers, the similarity in the trends of Figures 3.2 and 3.3 suggests that it can be a useful indicator of broad trends in long-term breeding numbers.

The above data were pooled into five year groups to facilitate statistical comparisons (Table 3.3) and there were significant differences between the mean numbers of eggs laid in these time periods (Kruskal-Wallis, χ^2_6=25.5, p<0.001).

Table 3.3
Summary data of number of eggs laid by Wandering albatrosses in five year periods from 1965 to 1999 on Macquarie Island

Time period	Northern eggs		Southern eggs		Total eggs	
	Mean	s.e.	Mean	s.e.	Mean	s.e.
1965-69	10.4	1.2	12.4	2.0	22.8	3.0
1970-74	3.2	0.6	11.0	0.8	14.0	0.5
1975-79	2.6	0.7	7.2	1.3	9.8	1.6
1980-84	1.6	0.5	4.2	0.7	5.8	0.9
1985-89	1.6	0.7	4.0	0.5	5.6	1.2
1990-94	1.6	0.2	5.2	0.4	6.8	0.4
1995-99	2.4	0.5	8.6	0.7	11.0	1.0

The number of eggs laid between 1980 and 1989 decreased significantly from the preceding 15 years (1965-1979) (χ^2_1=7.3, p<0.01). The number of eggs laid in the last ten years (1990-1999) represented a significant increase on the number of eggs laid in the 1980's (χ^2_1=5.61, p<0.02). However, the number of eggs laid in the last ten years was still significantly lower than the number of eggs laid between 1965 and 1979 (χ^2_1=13.7, p<0.001).

3.3.1.1b Non-breeding birds

Non-breeders were classified into three main breeding categories each year:

Adult-non-breeder – adult birds (>8 years of age) that had already bred
Adult-pre-breeder – adult birds that had not been recorded as breeding
Juvenile – immature or juvenile birds (< 8 years of age)

The make-up of the non-breeder population each year in the context of this classification regime is summarised in Table 3.4.

Table 3.4
Composition of non-breeding Wandering albatross population from 1995/96 - 2000/01

Season	Total number non-breeders [1]	adult non-breeder %	adult pre-breeder %	juvenile %
1995/96	14	0	21	79
1996/97	17	18	29	53
1997/98	19	21	21	58
1998/99	18	11	33	56
1999/00	21	19	43	38
2000/01	19	21	47	32

[1] includes only non-breeders of known age

Table 3.4 illustrates the dynamic composition of the non-breeding Wandering albatross population between 1995/96 and 2000/01. The composition is heavily influenced by the number of young adults who are yet to breed, being recruited into the breeding population, and the number of juveniles arriving back for the first time each season. The proportion of adult pre-breeders has increased while the proportion of juvenile birds has decreased over this time period. This is in part due to the relatively high number of young non-breeding birds that have formed pair bonds over the last three seasons and joined the breeding population. The decrease in the proportion of juvenile birds could also be an indication of decreasing fledgling survivorship, however, due to variation in the amount of time that this species spends at sea before returning to land, and the variation in the number of non-breeding birds in other categories, more data are needed to clarify such speculation.

There are few quantitative data on non-breeding Wandering albatross numbers before the start of the current study and comparable data are only available from 1995/96 to 2000/01. Data on the total number of non-breeders observed each day from the beginning of December to the end of March in each season were pooled and divided by the number of observation days (range 100-120) to calculate the mean number of birds observed each day (Figure 3.4).

Figure 3.4
Variation in frequency of non-breeding Wandering albatross resights at Caroline Cove, 1995/96 - 2000/01 (colours represent proportion of total non-breeders in each category)

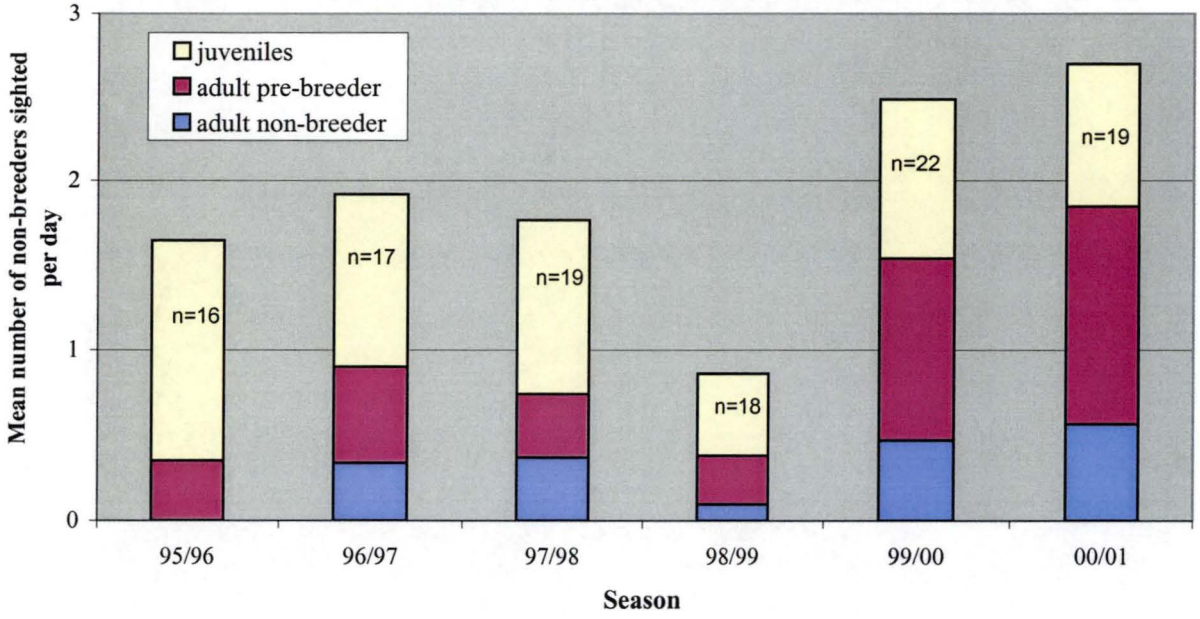


Figure 3.4 also shows the total number of non-breeding birds resighted each season and the proportion of birds in each non-breeding category.

The frequency of non-breeder sightings was dependent on the number of bird's involved in pair bonding, the prevailing weather conditions and observer effort. The relatively high frequency of re-sights in 1999/00 and 2000/01 are directly attributable to the number of non-breeders pair bonding in those years. In contrast, high proportions of juveniles and low proportions of adult-non-breeding birds are likely to result in fewer daily sightings of non-breeders (e.g. 1999/00). The total number of non-breeding birds identified each year was relatively consistent from 1995/96 to 2000/01 as non-breeding birds that were recruited into the breeding population were generally replaced by newly arrived birds.

Most non-breeders were resighted in three main areas of the south-western study area (Petrel Peak, Caroline Cove Amphitheatre and the Royal Penguin colony knoll. These areas represent good sites for potential nests or are already the location of breeding birds. Non-breeding birds returning to land for the first time were usually attracted to areas where other birds were congregating but new sites were occasionally utilised more frequently in seasons when a group of non-breeding birds arrived back together.

3.3.1.1c Age of breeding birds

Most Wandering albatross chicks on Macquarie Island have been banded each year since the 1960's and therefore most breeding birds are of known age. The youngest bird to arrive back at the natal colony during the present study was four years of age and the youngest recorded breeder over this time frame was eight years old. Age is calculated from the time of hatching, therefore chicks that hatched in March 2001 would be one year old in March 2002. The mean breeding age each season has remained relatively consistent throughout the current study ranging from 15.9 years in 1997/98 to 19.5 years in 2000/01 (Table 3.5)

Table 3.5
Mean breeding age of Wandering albatrosses each season from 1995/95 to 2000/01

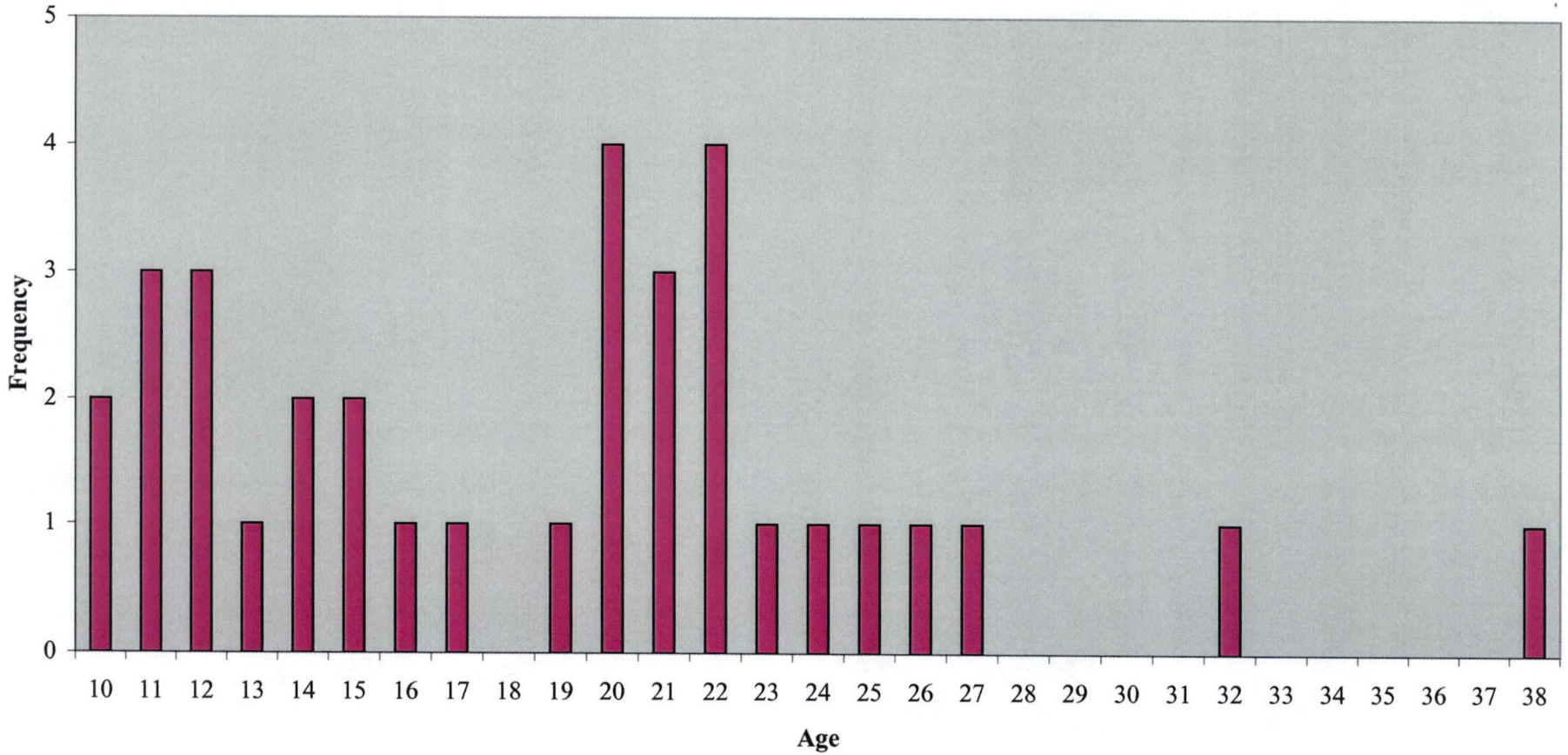
Season	Number of known age breeders	Min. age (years)	Max. age (years)	Mean breeding age (years)	Standard Error
1994/95	17	8	32	17.3	1.9
1995/96	16	9	27	16.3	1.2
1996/97	21	10	34	18.5	1.5
1997/98	16	8	35	15.9	2.0
1998/99	26	8	36	16.5	1.3
1999/00	13	10	31	16.8	1.6
2000/01	22	10	38	19.5	1.4

The age distribution of the entire current breeding population is shown below (Figure 3.5, 19 pairs, 34 known age breeders, mean =18.8 ± 1.1 (s.e) years, age taken at end of 2000). This distribution is irregular, almost bi-modal in nature, suggesting that there have been periods in the past when survivorship (particularly of fledglings and juveniles) was low. The are few birds over the age of 23 breeding in the current population and given the long-lived nature of this species this suggests that the survival of birds fledging prior to 1977 was very low. There are also relatively few birds aged between the ages of 16 and 19 but given the population trends of this species, this is more likely to be attributable to the low number of eggs laid (and consequently chicks fledged) in the mid 1980's.

3.3.1.2 Black-browed albatrosses: population trends

Comprehensive data on the number of breeding Black-browed albatrosses on Macquarie Island prior to the current study are rare.

Figure 3.5
Age distribution of Wandering albatrosses in the current breeding poppulation
19 breeding pairs, 34 known age breeders, mean = 18.1 ± 1.1 (s.e) years



Copson (1988) provided the best estimates in a study spanning seven years in the late 1970's and early 1980's. These estimates ranged from 14 to 27 eggs laid each year over this time period with a mean of 21 eggs.

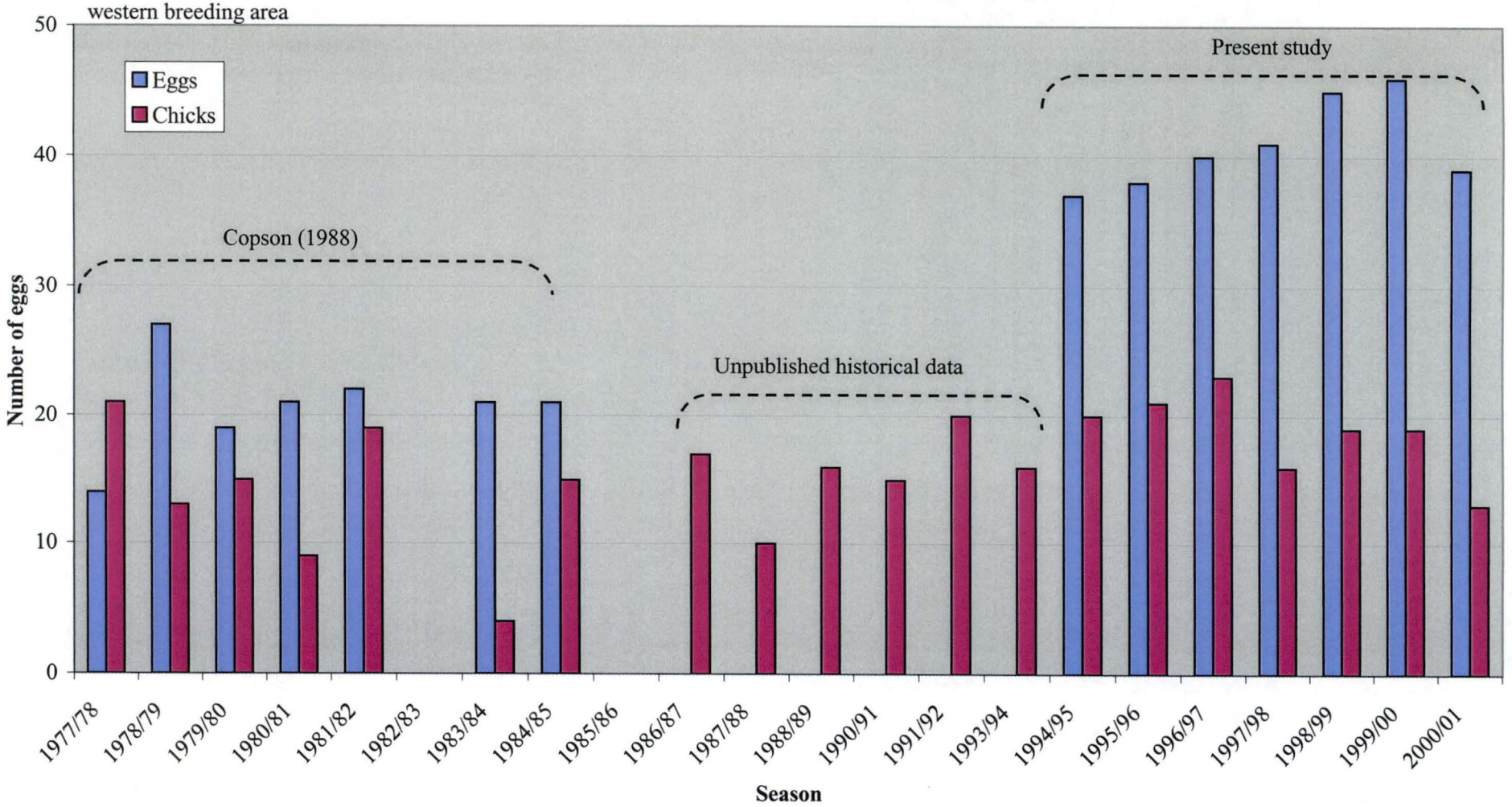
The field methodology utilised by Copson (1988) was less intensive than the present study since the south western colonies were first visited in October or November, followed by one or two visits in December and/or January and a final visit in March to band chicks. Due to the extended Black-browed laying period, it is likely that infrequent checks of this nature missed early or late breeders that laid and failed before the first or second visits. In addition, the degree of search effort used to collect the data described in Copson (1988) may have been different to the current study, and therefore potentially underestimated breeding numbers by 10-20% (based on number of cryptically nesting Black-browed albatrosses observed each season in the current study). Nevertheless, these data provided the only indication of Black-browed breeding numbers over that time period and are included in Figure 3.2.

From 1994/95 to 1999/00 Black-browed albatrosses breeding population increased by one or two pairs each year, increasing from 37 pairs in 1994/95 to a maximum of 46 pairs in 1999/00 (See Figure 3.6). In 2000/01 only 39 eggs were laid; however, four to six pairs exhibited typical pre-laying behaviour, but failed to lay eggs. The presence of these pairs indicated that the breeding population did not decrease significantly from 1999/00 to 2000/01. Breeding numbers of this magnitude represent a significant increase on breeding numbers reported by Copson (1988) in the south west colonies. However, Copson (1988) also described another small colony of Black-browed albatrosses breeding on North Head (one-two pairs each year between 1978 and 1984, no chicks fledged) and this colony had become extinct before the inception of the present study. Historical logbooks indicated that the North Head colony decreased from a high of 31 pairs in the early 1960's to no breeding pairs in the early 1990's. There was no evidence that Black-browed albatrosses breeding in the north of the island moved down to the southern end of the island to breed. Most of the breeders on North Head were banded and any movements would have been identified in the resight databases.

The number of chicks banded each year (unpublished data obtained from historical biological logbooks) is also shown in Figure 3.6. Due to variations in breeding success (eg see Chapter 4), the number of chicks surviving to banding each year is not an optimal or necessarily accurate method of ascertaining breeding numbers but can be used to identify large fluctuations (e.g. see Section 3.3.1.1a).

Figure 3.6

Number of eggs laid and chicks fledged by Black-browed albatrosses on Macquarie Island between 1977/78 and 2000/01 in the south-western breeding area



Breeding numbers appeared stable throughout the present study and the decrease from 1999/00 to 2000/01 appeared to be related to changes in breeding frequency, and possibly the pre-breeding condition of the potential breeders, rather than a decrease in breeding numbers due to increased mortality. There did not appear to be any trend in the number of chicks fledging each year from 1977/78 to the end of the present study and there was no significant difference between the average numbers fledged from 1978-1985, 1987-1994 and 1995-2001(Kruskall-Wallis: χ^2_2= 4.0, p=0.132, n.s).

Although several cohorts of chicks were banded prior to the start of the current study, most breeding birds were unbanded in the first year (1994/95) and therefore the majority of the current breeding population are of unknown age. Therefore, it was impossible to establish an accurate picture of the age distribution of the current breeding population. The youngest Black-browed albatross to return to land was resighted at four years of age while the youngest breeding bird resighted was five years old. The oldest recorded breeding bird was 29 years old, although there are several breeders that were banded as adults in the mid 1970's making them at least 30 years old.

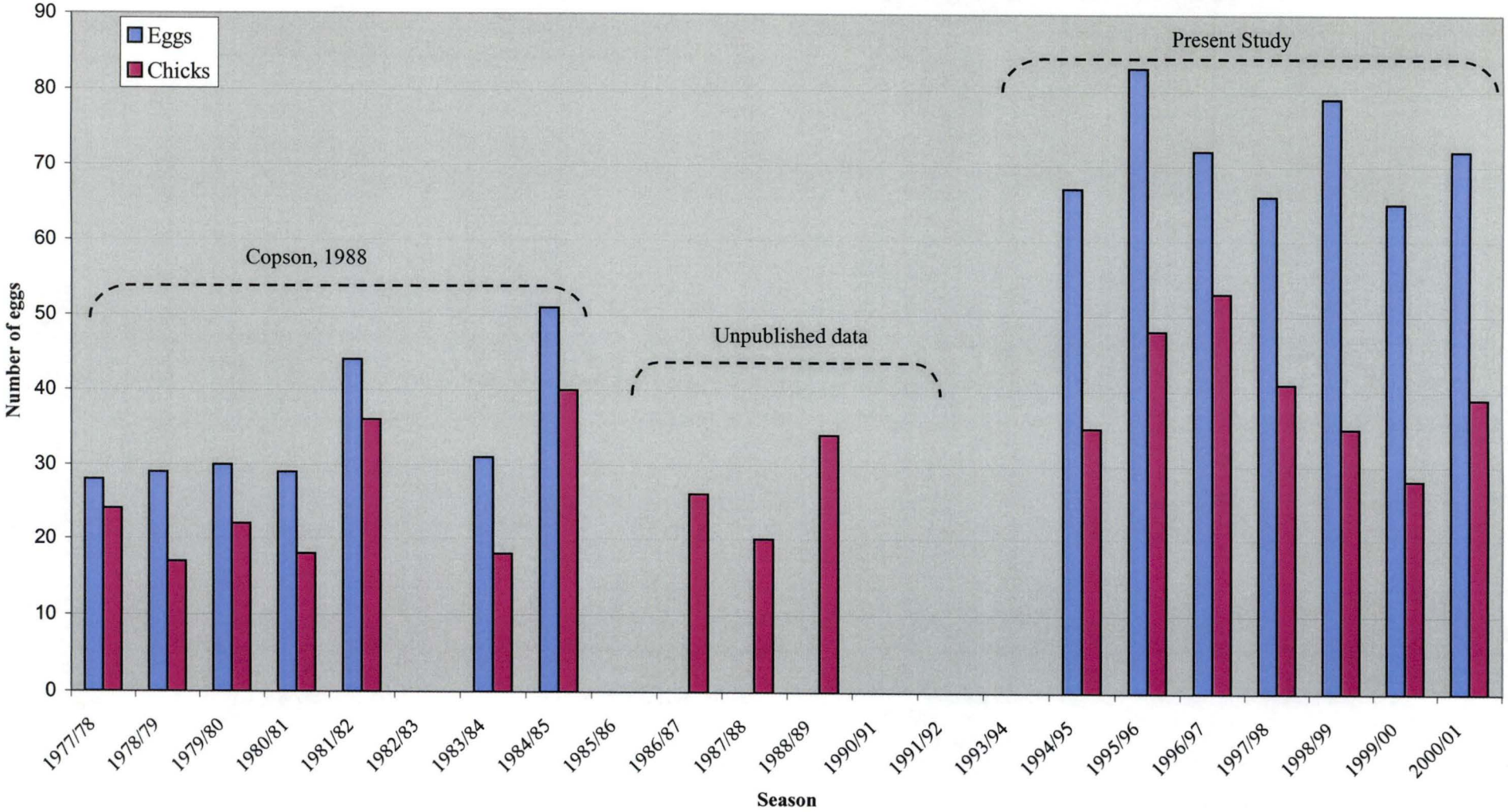
3.3.1.3 Grey-headed albatrosses: population trends

As with the Black-browed albatrosses, few comprehensive data exist on the number of breeding Grey-headed albatrosses breeding each year prior to the current study. Again, Copson (1988), provided the best estimates; however, due to the cryptic nature of many of the Grey-headed albatross nests it is possible that this study underestimated breeding numbers even more significantly than for Black-browed albatrosses. The number of chicks banded each year (assumed fledged) was also obtained from historical records, and both these data and data from Copson (1988) are included in Figure 3.7.

The number of eggs laid by Grey-headed albatrosses each year has remained relatively stable throughout the present study, and breeding numbers have fluctuated between 65 and 83 pairs over the last seven seasons (Figure 3.7). There was no clear trend in this variation and it is likely that fluctuations in breeding effort are related to changes in the breeding frequency of breeding birds (Chapter 5) as opposed to changes in survivorship and overall breeder numbers.

Figure 3.7

Number of eggs laid and chicks fledged each year by Grey-headed albatrosses on Macquarie Island between 1977/78 and 2000/01



The mean number of eggs laid increased significantly from 1977-1984 to 1994-2000 (Kruskal-Wallis, χ^2_1= 9.8, p=0.002); however, in contrast to the Black-browed albatrosses there were significant differences in the mean number of chicks that fledged each year from 1978-1985, 1987-1994 and 1995-2001 (χ^2_2= 7.0, p=0.03) and further tests revealed that these differences were attributable to a higher mean number of chicks fledged in the current study.

Similarly to Black-browed albatrosses, relatively few breeding Grey-headed albatrosses were of known age and it was not possible to get an accurate indication of the age distribution of the current breeding population. Known age breeders have ranged in age from nine to 23 years, although several breeders were banded as adults in the mid 1970's making them at least 30 years old. The youngest bird resighted in the study site was five years old (banded as a chick in 1996, resighted in 2001). Juvenile Grey-headed albatrosses were rarely resighted and only one or two were identified each year.

3.3.1.4 Light-mantled sooty albatrosses

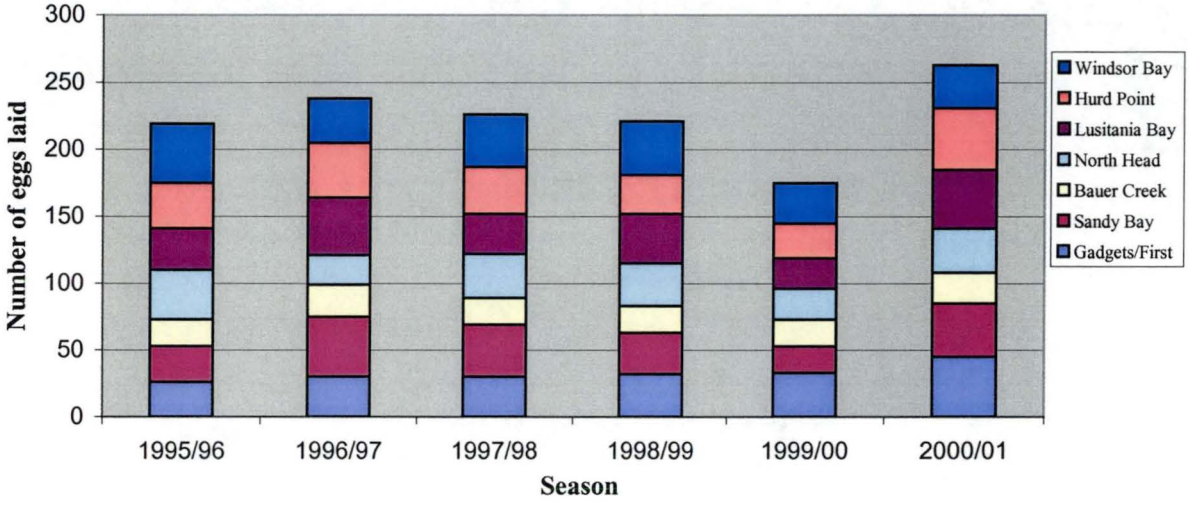
Although there have been intermittent studies on Light-mantled sooty albatrosses on Macquarie Island since the 1960's published data are rare. Historical data from biological logbooks are patchy and not directly comparable with data on breeding numbers from the current study (largely due to uncertainty about the boundaries of the sites). Therefore only data on population trends collected from the current study are presented here.

Table 3.6
Number of eggs laid by Light-mantled sooty albatrosses at seven Macquarie Island study sites between 1994/95 and 2000/01 (see Figure 2.4 for location of breeding sites)

Location	1994/95	1995/96	1996/97	1997/98	1998/99	1999/00	2000/01
Gadgets/First	27	26	30	30	32	33	45
Sandy Bay	37	27	45	39	31	20	40
Bauer Creek	25	20	24	20	20	20	23
North Head		37	22	33	32	23	33
Lusitania Bay	37	31	43	30	37	23	44
Hurd Point		34	41	35	29	26	46
Windsor Bay	26	44	33	39	40	30	32
Total (1995/96-) 7 sites		219	238	226	221	175	263
Total (1994/95-) 5 sites	152	148	175	158	160	126	184

The number of Light-mantled sooty albatross eggs laid at seven study sites around the island is shown in Table 3.6 and illustrated graphically in Figure 3.8. Five of the study sites were monitored in 1994/95 so totals are provided for all sites from 1995/96 onwards and five sites from 1994/95 onwards. The total number of eggs found each year has remained relatively stable and there were no significant differences in the number of eggs laid at each site between years (Kruskal-Wallis, $\chi^2_6 = 9.38$, p=0.132, ns)

Figure 3.8
Number of eggs laid each year by Light-mantled sooty albatrosses at seven study sites around Macquarie Island from 1995/96 to 2000/01 (see Figure 2.3 for sites)



The decrease of breeding numbers in 1999/00 followed by an increase in 2000/01 is typical of changes in breeding frequency and therefore reflects annual breeding effort rather than changes in actual population numbers (see Chapter 5).

A relatively high proportion of Light-mantled sooty albatrosses breeding in the northern study sites (specifically North Head, Bauer Creek and Gadget and First Gullies) were banded prior to the current study. However, the available banding records were incomplete and as few published data exist, only limited use has been made of this information to date. However, banding records of several birds in the current breeding population were found. These birds were banded as adults in the late 1960's making them at least 30-40 years old. The youngest Light-mantled sooty albatross to return to its natal colony was resighted in the 2000/01 season and was four years of age. Four juveniles birds (<7 years) old were resighted in 2000/01 and all were positively identified by their coloured darvic bands.

3.3.2 Survivorship

3.3.2.1 Overview

Six datasets were utilised in the survivorship analyses. Table 3.7 summarises the time frame covered and the number of encounter histories (i.e. individual birds) contained in each dataset.

Table 3.7
Temporal extent and number of encounter histories in each of the six datasets used in the survivorship analyses of Wandering, Black-browed and Grey-headed albatrosses

Dataset	Acronym	Time Period	# birds
Wandering albatross banded as chicks	WA-BAC	1955-1995	319
Wandering albatross banded as adults	WA-BAA	1955-2000	153
Black-browed albatross banded as chicks	BB-BAC	1974-1995	289
Black-browed albatross banded as adults	BB-BAA	1976-2000	142
Grey-headed albatross banded as chicks	GH-BAC	1974-1995	722
Grey-headed albatross banded as adults	GH-BAA	1976-2000	442

3.3.2.2 Goodness of Fit Tests

Goodness of Fit tests (GOF) were used to test the assumptions of the basic CJR model and an age-dependent, time-dependent model. In each case GOF tests were only applied to the global models, with fully time dependent parameters and the results are presented in Table 3.8.

The assumptions inherent in the global CJR model ($\Phi(t).p(t)$) were violated when this model was applied to the 'banded as chicks' datasets (all species). This is attributable to differences between adult and fledgling survivorship as indicated by the good fit of the age-dependent, time dependent model to the data. Age-dependent, time-dependent models fitted all data sets except the GH-BAA. The global CJR model also did not fit this dataset and it is likely that there are too few resights in this database to allow any model to be fitted.

Table 3.8
Summary results of GOF tests on the time dependent global model [Φ(t) p(t)] and the age and time dependent global model [Φ{(1stR(t) 2ndR(t)} p(t)]

Dataset	Φ(t) p(t)	Φ{(1stR(t) 2ndR(t)} p(t)
WA-BAC	$p < 0.01$ *	$p > 0.2$
WA-BAA	$p > 0.2$	$p > 0.2$
BB-BAC	$0.01 < p < 0.02$*	$0.07 > p > 0.08$
BB-BAA	$0.07 > p > 0.08$	$p > 0.1$
GH-BAC	$0.02 > p > 0.03$*	$p > 0.2$
GH-BAA	$p < 0.01$ *	$p < 0.01$*

* indicates that model deviance was too high, therefore model does not fit the data

The fit of the age-dependent, time dependent model to the other two 'banded as adults' datasets provides evidence of a significant difference between survivorship to the first resight after banding and survivorship to subsequent resights.

3.3.2.3 Fitting models using Akaike's Information Criterion (AICc)

At the completion of the above GOF tests, variations on the above models were fitted to the five datasets (GH-BAA omitted due to GOF results – See Appendices 3.1a-3.1e for MARK 2.1 results)

In all cases the most parsimonious models had time-dependent re-capture probability. The most parsimonious model fitted to the WA-BAC dataset had time-dependent fledgling survivorship and constant adult survivorship. In contrast, the model that best fitted the Black-browed and Grey-headed BAC datasets had constant fledgling survivorship and constant adult survivorship over time. In the case of WA-BAA and BB-BAA where the GOF tests suggested both types of models fitted these data, AICc values indicated that the model with time-dependent survivorship to the first re-capture and constant survivorship thereafter was the

most parsimonious model in both cases. However, Burnham and Anderson (1998) suggested that differences in AICc values of magnitude ~1-2 did not necessarily represent significant differences between models. Therefore it was not possible to determine the most parsimonious model fitted to the BB-BAA dataset (Appendix 3.1e) on the basis of the AICc values.

3.3.2.4 Likelihood Ratio Tests

Likelihood ratio tests (LRT) were used to further assess differences between nested models. Tests were performed on all models that fitted the data regardless of the AICc rank. This allowed comparisons to be made between the two methods of model selection. The results of the LRT are summarised in Appendix 3.2 and are generally very similar to the results of model selection using AICc values. For example, in all cases LRT showed that time dependent re-capture probability was fundamental to the most parsimonious models. There was strong evidence that Wandering albatross fledgling survival varied over time, less conclusive evidence that Grey-head fledgling survivorship was time dependent and no evidence of variation in the survivorship of Black-browed fledglings. However, there was some evidence that the survivorship of adult Black-browed albatrosses was time dependent. This evidence was not conclusive as it was only shown by the BB_BAC dataset, not the BB_BAA dataset.

When the basic CJR models were fitted to the 'banded as chicks' datasets there was evidence that the survivorship of adult Wandering albatrosses was time dependent (Appendix 3.2d). However, there was little evidence that the age dependent model, where survivorship to the first re-sight was calculated independently of survivorship to subsequent resights, fitted the data any better.

LRT showed that if age dependent models were fitted to the data, then those with time dependent survivorship to first re-capture had a significantly better fit. As there was little evidence that this type of model fitted the data better than the CJR model it is difficult to draw definitive conclusions from these results. A similar situation was observed for the BB-BAA dataset (Table 3.10e). There was no evidence that overall survival rates varied over time (CJR model) and no evidence that the age-dependent model fitted the data better. Similarly to the WA-BAA, when these age dependent models were tested on the BB-BAA, there was some evidence that survival to the first resight was time dependent.

3.3.2.5 Estimates of survivorship

Mean values of survivorship were estimated from each dataset using the highest AICc ranked models (Tables 3.9 and 3.10). As the above GOF and LRT tests suggested, adult survivorship was significantly higher than fledgling survivorship for each species. Grey-headed albatrosses had the most dichotomous survivorships with the highest adult survivorship (96.7±1.1%) and the lowest fledgling survivorship (33.6±4.6%). Wandering albatrosses had the next highest mean adult survivorship (95.3±0.6%) and Black-browed albatrosses had the lowest of 91.5±1.1%.

Table 3.9
Adult survivorship of Wandering (1955-2000), Black-browed and Grey-headed albatrosses (1976-200) on Macquarie Island

Dataset	Time frame	Adult survival (%)	S.E (%)	Model	AICc rank
Wandering albatross					
WA-BAC	1955-1995	95.3	0.6	Φ{fl(t) ad(.)} p(t)	1
WA-BAA[a]	1955-2000	91.0	0.7	Φ(.) p(t)	3
WA-BAA[b]	1955-2000	92.4	3.3	Φ{1stR(.) 2ndR(t)} p(t)	4
WA-BAA[c]	1955-2000	90.8	0.8	Φ{1stR(t) 2ndR(.)} p(t)	1
Black-browed albatross					
BB-BAC	1974-1995	91.5	1.1	Φ{fl(.) ad(.)} p(t)	1
BB-BAA[a]	1976-2000	90.3	1.1	Φ(.) p(t)	2
BB-BAA[b]	1976-2000	90.1	3.5	Φ{1stR(.) 2ndR(.)} p(t)	3
BB-BAA[c]	1976-2000	89.7	1.2	Φ{1stR(t) 2ndR(.)} p(t)	1
Grey-headed albatross					
GH-BAC	1974-1995	96.7	1.1	Φ{fl(.) ad(.)} p(t)	1

[a] mean survivorship, [b] survivorship to first recapture, [c] survivorship to all subsequent resights

When calculated from the 'banded as chicks' datasets, the adult survivorship of Wandering albatrosses was higher than any of the survival estimates calculated from the 'banded as adults' dataset. The reasons for this difference are unclear but it could be attributable to adult birds becoming more wary of people post banding (and subsequently less likely to be resighted) than birds that were banded as chicks. Adult survivorship to first re-sight was

slightly higher than the survivorship to subsequent resights; however, in the context of the model AICc values and LRT tests this difference was not significant. Adult survivorship of Black-browed albatrosses was also slightly higher when calculated using the BB-BAC dataset in comparison to the BB-BAA dataset, although again this difference appeared to be insignificant in the context of the AICc model selection and the standard errors around these values (Table 3.9). There was no significant difference between the survivorship of adult Black-browed albatrosses to their first resight post-banding relative to their survivorship to subsequent resights.

Table 3.10
Fledgling survivorship of Wandering (1955-1995), Black-browed and Grey-headed albatrosses (1976-1995) on Macquarie Island

Species	Dataset	Time Frame	Fledging survival (%)	S.E. (%)	Model	AICc rank
Wandering albatross	WA-BAC	1955-1995	45.9	3.5	Φ{fl(.) ad(.)} p(t)	2
Black-browed albatross	BB-BAC	1976-1995	58.5	5.8	Φ{fl(.) ad(.)} p(t)	1
Grey-headed albatross	GH-BAC	1976-1995	33.6	4.6	Φ{fl(.) ad(.)} p(t)	1

Black-browed albatrosses showed the highest mean fledgling survivorship (58.5±5.8%), almost double that of the Grey-headed albatrosses (33.6 ± 4.6%). Wandering albatross fledglings had a mean survivorship of 45.9±3.5% over the 40 year time frame and this estimate was also the least variable. However, estimates of fledgling survivorship were generally more variable than estimates of adult survivorship.

3.3.2.6 Variation in survivorship over time

There was little conclusive evidence for time-dependent survivorship of adults and fledglings in Black-browed and Grey-headed albatrosses (Sections 3.3.2.3, 3.3.2.4). However, there was strong evidence that the Wandering albatross fledgling survivorship varied significantly

between 1955 and 1995, and also some evidence (although less conclusive) that adult survivorship varied over this time period.

The most parsimonious model fitted to the WA-BAC dataset was $\Phi\{fl(t)\ ad(.)\}\ p(t)$, suggesting that juvenile survivorship was time-dependent but adult survivorship was not. However, the best model to fit the WA-BAA dataset was $\Phi\{1stR(t)\ 2ndR(.)\}\ p(t)$ and this indicated that there was some degree of time-dependence in the survivorship of adults. LRT also provided some evidence that adult survivorship of Wandering albatrosses was time-dependent.

While the mark-recapture software used in this study can provide annual estimates of survivorship, they are only estimates of 'apparent survivorship' (i.e. a function of both survivorship and re-capture probability) and thus may not necessarily reflect the true survivorship of that year (White and Burnham 1999). Therefore the time-dependence of Wandering albatrosses survivorship was examined in two ways:

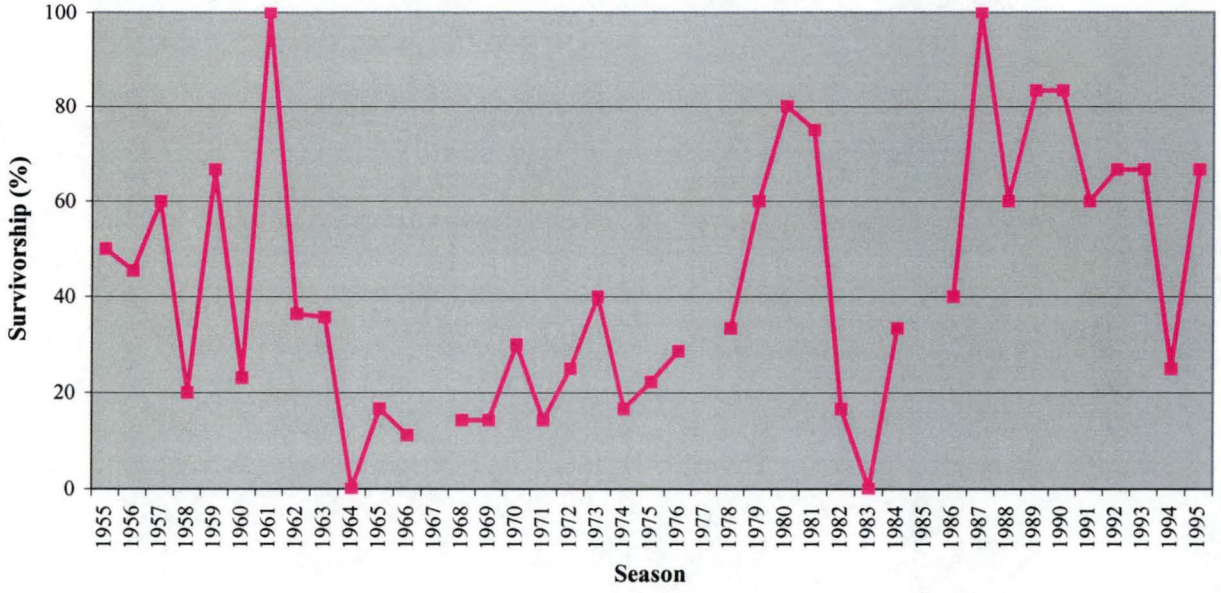
1. The fledging survivorship of chicks in each year was calculated manually using the WA-BAC dataset (Figure 3.9).

2. The 45 year dataset (WA-BAC) was partitioned into four ten year periods and fledgling and adult survivorship were calculated independently in each of those periods (Figure 3.10).

3.3.2.6a Annual variation in fledgling survivorship of Wandering albatrosses (1)

Manual calculation of annual survivorship is only possible for parameters such as fledgling survivorship where iterative processes are not required. Therefore it was not possible to calculate annual adult survivorship in this way. Survivorship was only calculated for years where more than one chick fledged and therefore survivorship was not estimated in 1967, 1977 or 1985 (Figure 3.9). Annual fledgling survivorship decreased sharply in the early 1960's and remained at or below 40% for the next 16 years. Survivorship rose above 40 % between 1979 and 1982 before decreasing again between 1982 and 1986. Following this, survivorship increased again and became relatively stable after 1988. Due to the small number of chicks fledging each year (no more than 15 recorded each year since 1955) the non-return of one or two chicks from each year often had a significant impact on year-to-year fluctuations. Therefore, the mean survivorship was also calculated over ten year periods in order to clarify any long-term trends (Section 3.3.2.6b, Figure 3.10).

Figure 3.9
Variation in survivorship of Wandering albatross fledglings from 1955 to 1995



3.3.2.6b Long-term time-dependent trends in survivorship of Wandering albatrosses (2)

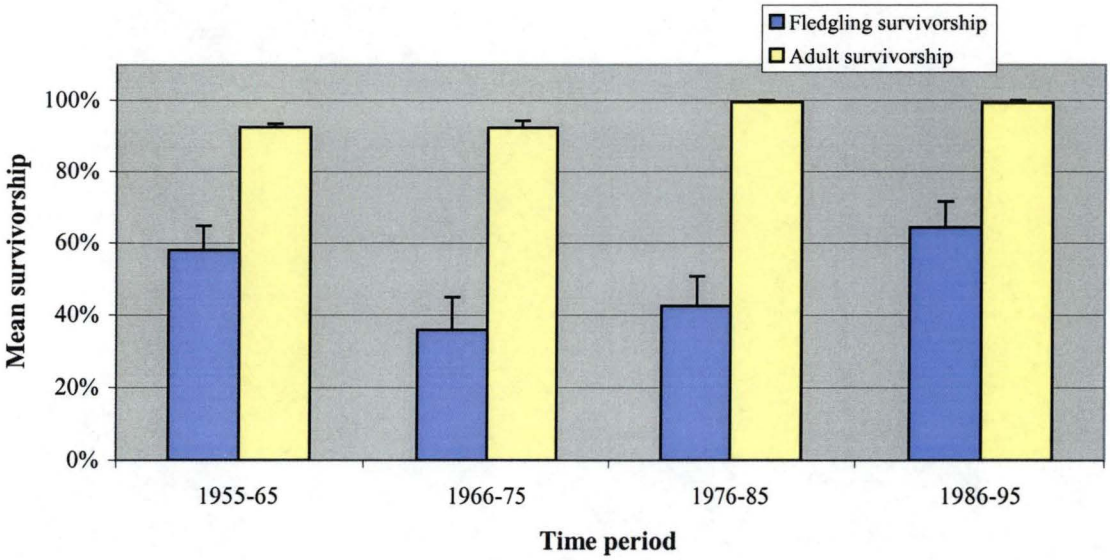
The model Φ{fl(.) ad(.)} p(t) was used for each ten year time period and GOF tests were used to ensure the fit of each model to the datasets. In all cases there was no evidence that the model deviance was significantly higher than the bootstrap simulations ($p > 0.1$ in each case, n.s) indicating that the models used fitted the data adequately.

Fledgling survivorship decreased sharply from 58 % in the time period 1955-1965 to 36 % in 1966-1975. Survivorship increased slightly in 1976-1985 (43%) and increased again to its highest ten-year level in 1985-1995 (64%). Adult survivorship showed a different trend with lower estimates between 1955 and 1975 (92 %) and higher estimates between 1976 and 1995 (99 %). There was considerably more variation in the estimates of fledgling survivorship relative to the estimates of adult survivorship.

3.3.2.7 Immigration, emigration and philopatry

An important assumption of the survivorship analyses is that the populations are closed, that is there is no immigration or emigration and therefore any birds that are not re-sighted are considered to have died.

Figure 3.11
Mean fledgling and adult survivorship of Wandering albatrosses on Macquarie Island



Similarly the calculation of fledgling survivorship depends on the return of fledglings to their natal colony. Philopatry amongst Procellariiformes is well developed and once an albatross has bred in a particular location, it rarely moves vast distances to another (Warham 1990; Prince *et al.* 1994; Moore 2001).

There are few data on the immigration, emigration or colony fidelity of Wandering, Black-browed and Grey-headed albatrosses from Macquarie Island. A single Wandering albatross banded on Macquarie Island was re-sighted at Heard Island in the 1970's (Johnstone 1980); however, the breeding status of this bird was uncertain. No other resights of adult Wandering albatrosses from Macquarie Island at other locations have been recorded. One or two unbanded Wandering albatrosses are generally observed each season on Macquarie Island and it is likely that these birds are visitors from other locations. Very few of these birds were resighted again subsequent to their initial re-sight and banding so the actual level of recruitment of true immigrants into the breeding population is likely to be very low. It is difficult to quantify this level of potential immigration accurately as genetic analyses are required to conclusively identify birds from other locations.

Similarly, immigration into the Black-browed and Grey-headed albatross breeding populations also appears to be limited on Macquarie Island. There is currently one female Black-browed albatross breeding on Macquarie Island that was banded as a chick on Iles Kerguelen in 1990. There is no conclusive evidence that any Grey-headed albatrosses

currently breeding on Macquarie Island are from other locations. A juvenile Grey-headed albatross banded on South Georgia in 1991 was resighted in 1997/98 on Macquarie Island but not re-sighted again in subsequent seasons.

Emigration from Black-browed and Grey-headed albatross breeding populations is more likely to be a important issue, particularly with the Black-browed albatrosses in view of the relatively large colony (>100 pairs) of breeding birds only 37 kilometres to the south of the Macquarie Island colony. It is feasible that returning Black-browed fledglings (or even adults that are yet to breed) are attracted to this high density of nesting birds and if this occurred, survivorship would be underestimated. In the single detailed census of these islets a single Black-browed albatross banded on Macquarie Island was observed (N. Brothers, unpublished data). Another Black-browed albatross banded as an adult on Macquarie Island was also observed breeding on Campbell Island in the 1990's (Moore *et al.* 1997). There are no conclusive records of returning Wandering or Grey-headed albatross fledglings from Macquarie Island breeding at other locations.

3.3.2.8 Long-line fishing effort between 1955 and 1995-implications for survivorship of Wandering albatrosses

Long-line fishing is not permitted in the Macquarie Island Economic Exclusion Zone and (legal) fisheries in this area have been restricted to a single license to trawl for Patagonian Toothfish (*Dissostichus eleginoides*) each year (Environment Australia 2001b). Nevertheless, there is evidence that long-line fishing in distant waters has had an impact on Macquarie Island albatrosses, particularly Wandering albatrosses (de la Mare and Kerry 1994) and therefore an attempt was made to further examine the relationship between survivorship and long-line fishing effort. Long-line fishing data between 1955 and 1995 were obtained for discrete areas around the southern hemisphere between 30°S and 60°S. These data were in the form of number of hooks set each year and were collated from tuna fishing fleets of all nationalities (see Section 3.2.2.4). Long-line fishing for tuna was the most common form of long-lining over this time period (Brothers *et al.* 1999) and these were the only data used to plot Figures 3.11a-c. Survivorship estimates obtained from the analysis of long-term trends in Wandering albatross fledgling survivorship (Section 3.3.2.6b, Figure 3.10) are also superimposed on these figures.

The first major decrease in fledgling survivorship of Wandering albatross (1962-1964 – see Figure 3.11a) coincided with the beginning of long-line fishing for tuna in the Southern Hemisphere. Hook numbers increased rapidly in all oceans through the 1960's coinciding

with the lowest 10-year fledgling survivorship. Excluding the massive fishing effort in 1975 (203 million hooks set), hook numbers in the Pacific ocean showed a gradual increase from the start of fishing to the 1960's up until the mid 1990's when it began to decline. A similar pattern of increasing hook numbers was observed in the Atlantic Ocean; however the number of hooks set did not start any real decline until 1998 and 1999 (Figures 3.11a and 3.11c). A different trend was observed in the Indian Ocean fishery where hook numbers peaked in the mid-1980's, then declined in the early to mid-1990's before increasing again in the late 1990's (Figure 3.11b). The number of hooks set in this fishery declined significantly from approximately 80 million hooks set in 1999 to less than 10 million hooks set in 2000.

On the basis of the broad spatial scales examined, it appears that the number of hooks set in the Indian Ocean region was negatively correlated with the fledgling survivorship of Wandering albatrosses from Macquarie Island. Specifically, the number of hooks set in the eastern Indian Ocean, between 80°E and 140°E appear to be the most closely linked to the variation in fledgling survivorship. The gradual increasing trend of hooks set each year in the Atlantic and Pacific Oceans throughout the 1960's, 1970's and 1980's do not seem to be related to the fluctuations observed in the fledgling or adult survivorship of Wandering albatrosses on Macquarie Island. In addition to broad scale comparisons, Spearman Rank Correlation Tests were also used to test for correlations between the numbers of hooks set each year and annual fledgling survivorship (Section 3.3.2.6a). No significant correlations were found and it is likely that the large inter-annual fluctuations in conjunction with the large spatial areas covered by the hook set data combined to mask any significant relationships. It is almost impossible to quantify the extent of illegal or unreported fishing activity that occurred during this time period (Tuck and Bulman 2001) and it is possible that impacts of these vessels also contributed to the lack of correlation between apparent fishing effort and survivorship.

There was no obvious relationship between the lower adult survivorship from 1955-1975, relative to 1975-1995 and the long-line fishing effort documented in Figure 3.11a-c. In a similar manner to the fledgling survivorship, it is likely that the spatial scales of hook set data were too large to relate directly to variations in adult survivorship. Again it is possible that other fisheries or the impact of unregulated or illegal fisheries also served to mask any correlations

Figure 3.11a

Number of hooks set each year in the Southern Hemisphere tuna long-line fishery
(shaded columns represent Wandering albatross fledgling survival for decades 1956-65, 1966-75, 1976-85, 1986-95)

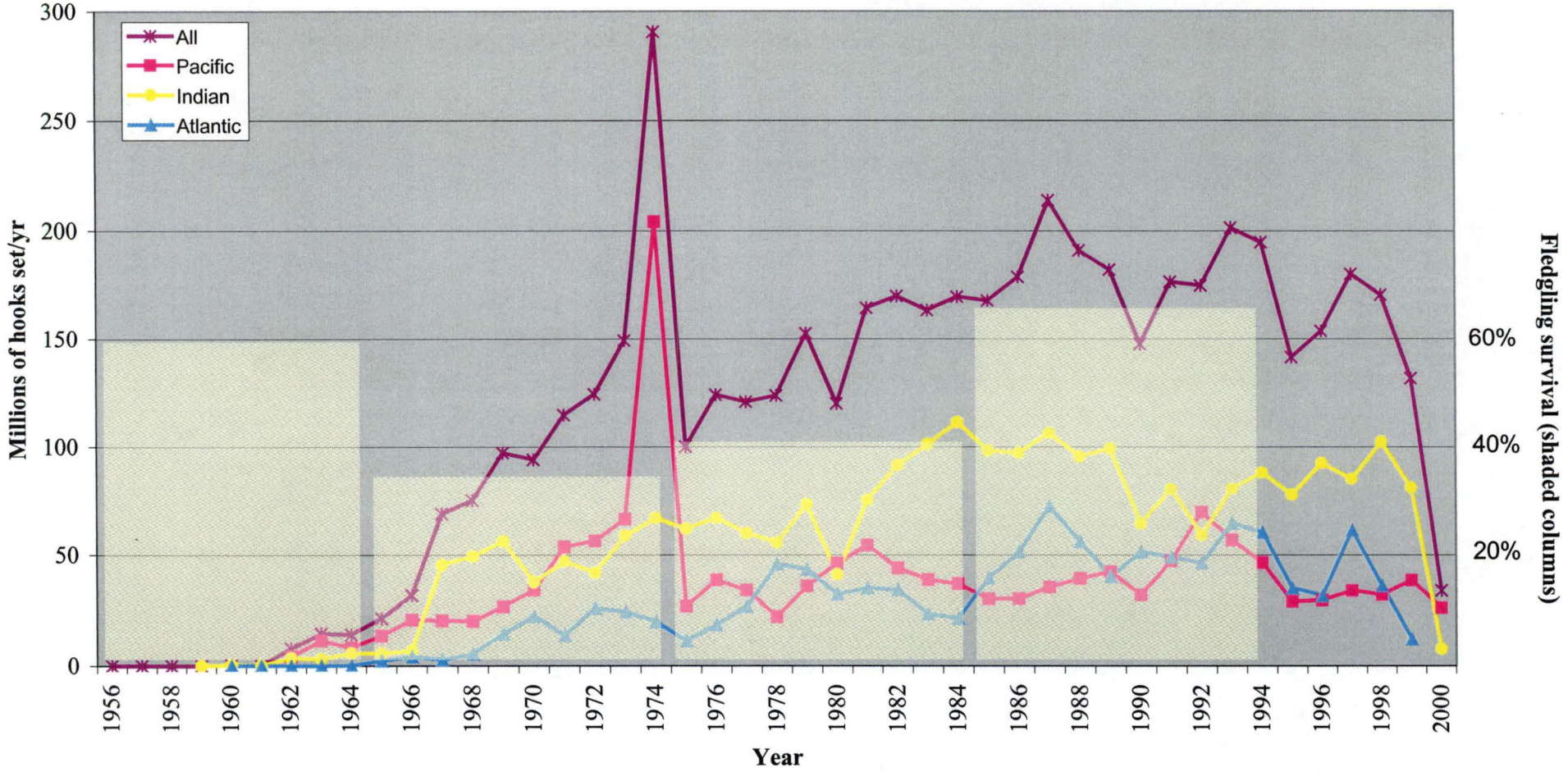


Figure 3.11b

Number of hooks set each year in the Indian Ocean tuna long-line fishery
(shaded columns represent Wandering alabtross fledgling survival for decades 1956-65, 1966-75, 1976-85, 1986-95)

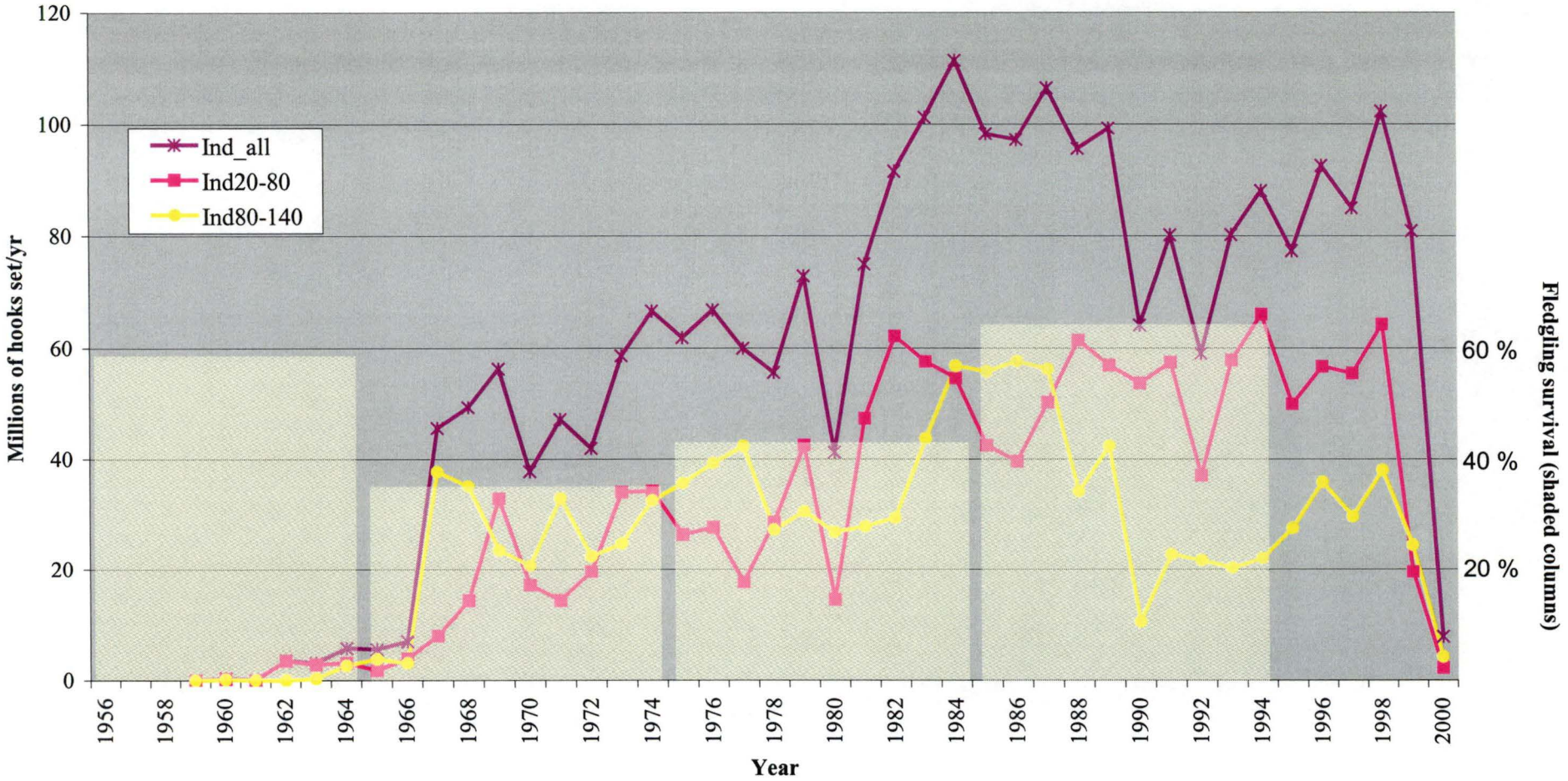
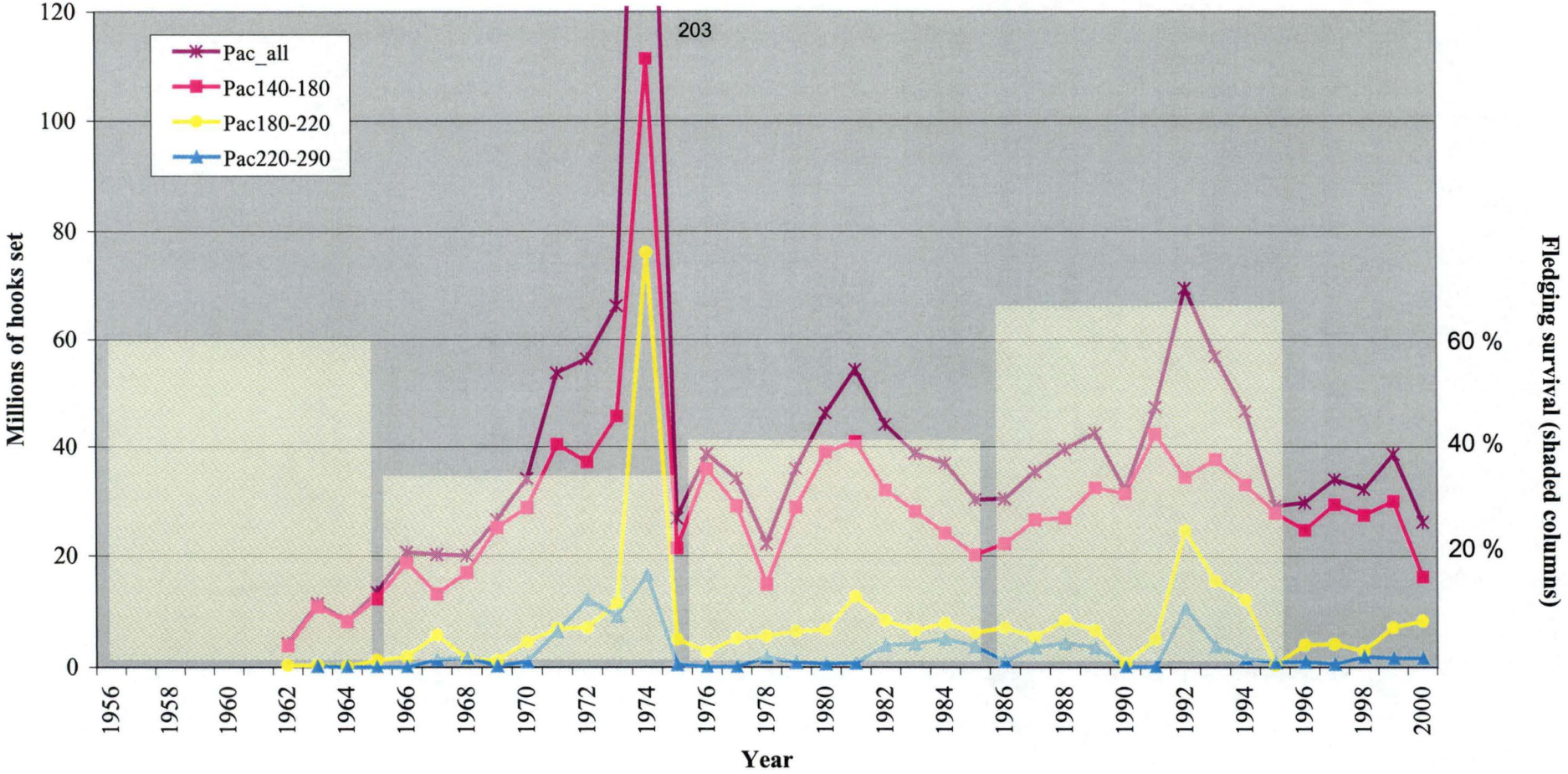


Figure 3.11c

Number of hooks set each year in the Pacific Ocean long-line fishery
(shaded columns represent Wandering albatross fledgling survival for decades 1956-65, 1966-75, 1976-85, 1986-95)



3.4 DISCUSSION

3.4.1 Population trends

3.4.1.1 Comparison between species

Data on annual breeding numbers of albatrosses on Macquarie Island were obtained from 1955-2000 for Wandering albatrosses (with anecdotal records spanning the last 100 years); 1978-2000 for the Black-browed and Grey-headed albatrosses (significant gaps in the records) and from 1994-2000 for the Light-mantled sooty albatrosses. The most comprehensive data on breeding numbers were obtained for the Wandering albatrosses. The large size of this species in conjunction with conspicuous nesting sites, seemingly docile nature and small breeding population has made it the subject of much interest since ANARE (Australian National Antarctic Research Expeditions) colonised Macquarie Island in the 1950's, and therefore breeding numbers have been recorded relatively accurately each year. Comprehensive quantitative data were only collected on non-breeding Wandering albatrosses since 1994/95 and few quantitative data on non-breeders from other species were obtained.

3.4.1.1a Wandering Albatrosses

Following the demise of the population at the hands of the sealers and the subsequent increase to a peak in the early 1960's (Carrick and Ingham 1970) the Macquarie Island Wandering albatross population again declined significantly to be at levels close to extinction in the mid 1980's. Tomkins (1985b) calculated a high mortality rate of adults between 1974 and 1978 and reported that 31 banded breeding birds disappeared (assumed dead) during this time period. However, Selkirk *et al.* (1990) noted that several of these birds were resighted subsequent to this study, emphasising the caution that needs to be exercised when estimating survivorship over short time periods. de la Mare and Kerry (1994) documented a similar decrease to that reported here and suggested that it could be linked to elevated mortality levels caused by interactions with tuna long-line fisheries. The current age distribution of breeding birds on Macquarie Island is indicative of increased mortality levels of juveniles prior to 1980 and recent survivorship analyses also provide evidence of increased mortality of young birds during the 1960's and 1970's (see also section 3.4.1.3).

Human disturbance on Macquarie Island may also have played a role in the decline of the Wandering albatross breeding population throughout the 1960's and 1970's. Anecdotal reports obtained from biological logbooks indicate that sustained invasive research (e.g. removal of egg, birds and/or chicks from nests) occurred during this time period which may

have impacted upon nest and pair fidelity and consequently breeding success and breeding frequency. Wandering albatrosses are an iconic species and are remarkably photogenic, and therefore expeditioners have often visited their breeding sites frequently throughout the last 50 years. During the 1980's researchers became more aware of the potential impact of people of the breeding behaviour of Wandering albatrosses and most intrusive research stopped around this time (de la Mare and Kerry 1994). In 1986, the Department of Primary Industry Water and Environment, Tasmania instigated a closure of the main breeding grounds in the south-western corner of Macquarie Island from December to March inclusive each year (see Figure 1.2). This closure was extended to run from November to April inclusive after the first year of the current study (1994/95) to further reduce disturbance to breeding birds on eggs and courting/pair-bonding non-breeders.

This closure has been an important factor in the recovery of the breeding population, and the number of eggs laid in the last ten years was significantly higher than during the 1980's. Fledgling survivorship increased between 1985 and 1995 and the number of birds returning to the breeding colonies increased significantly during this time period. The closure was likely to be instrumental in allowing newly arrived birds to form pair bonds and therefore be recruited into the breeding population more rapidly. Most of the increase in breeding numbers was attributable to an increase in the number of breeding birds at the south-western breeding sites. The number of breeding birds at the north western breeding sites has not increased by the same degree since 1986 and this may be more evidence of the positive impact of the closure. Since 1997, human disturbance to breeding Wandering albatrosses at the northern breeding sites has been significantly reduced, which may facilitate the formation of new pair bonds and eventually an increase in the breeding population. However, there have been so few chicks fledged from this area in the last 15 years that returning fledglings are rare, and those that do return to Macquarie Island are often attracted to the high numbers of birds inhabiting the south-western corner.

Following the relatively rapid increase in breeding numbers from 1986 to 1994, the number of breeding pairs has remained stable at approximately 19 pairs since the beginning of the current study in 1994/95. Most experienced breeders that have not returned have been replaced by young breeding birds within one or two years. The number of breeding pairs has fluctuated considerably between years (e.g. 1998/99 - 15 breeding pairs and 1999/00 - seven breeding pairs) this being largely attributable to high breeding success in 1996/97, low breeding success in 1997/98 and relatively high breeding success in 1998/99. Interactions between breeding success and breeding frequency can often make breeding population estimates difficult for biennial breeding species and consequently multi-year monitoring

programs such as the present study are vital in accurately determining current population levels.

The number of non-breeding Wandering albatrosses has also remained relatively stable between 1994/95 and 2000/01 and non-breeding birds that become breeders are usually replaced in the same year by newly recruited birds. During 1999/00 and 2000/01 there were high numbers of non-breeders courting and forming strong pair bonds, indicating that there is potential for an increase in the breeding population over the next two to three years. The number of birds that are pair bonding in each season is largely responsible for variations in the average number sighted each day. Pair bonding birds attend their nest site more regularly than other non-breeders, particularly in the year before they breed. Weather patterns also play an important role in the daily number of sightings of non-breeders and birds are most often seen when winds are from the south-west, west or north-west between 20 and 30 knots.

Observations of non-breeders on Macquarie Island since 1994/95 correspond with patterns and behaviour reported by Pickering (1989) on Bird Island, South Georgia. Recruitment into the breeding population generally takes between two to five years after a bird has first returned to the island. Pair-bonding birds arrive earlier and spend more time ashore than other non-breeding birds and typically leave the island mid-season compared to younger birds, which tend to came ashore more sporadically throughout the season.

3.4.1.1b Black-Browed albatrosses

The number of breeding Black-browed albatrosses reported in the current study is significantly higher than that reported by Copson (1988) in the late 1970's and early 1980's. It is likely that the increase observed in breeding numbers from that study to the current study is more attributable to differences in census methodology and timing than an actual significant increase in breeding numbers. The number of chicks fledging each year was shown to be a good indicator of broad population trends in the Wandering albatross analyses (Section 3.3.1.1a) and the number of Black-browed chicks that fledged each year from 1978 to 2001 was relatively consistent. Further evidence that the Black-browed albatross breeding population was stable between 1978 and 2001 was provided by statistical tests that indicated there were no significant differences between annual numbers of chicks that fledged prior to 1994/95 and the number fledged between 1994/95 and 2000/01.

The small breeding population of Black-browed albatrosses on North Head declined from 31 breeding pairs in the 1950's to less than three breeding pairs in the late 1970's (Copson 1988).

Most of this decline occurred in the 1960's and 1970's and in the absence of detailed population data it is difficult to ascertain the causes of such a decline. It is possible that due to its proximity to the main station, this small Black-browed colony declined due to direct human disturbance. Consistent human disturbance could impact on pair formation, attendance patterns and breeding success and if continued over a long enough time period such disturbance could be responsible for the demise of a small colony. It is also possible mortality due to long-line- fishing also played a part in the decline of this small population; however, without population data from the south-western colony this hypothesis is impossible to substantiate. In contrast, there is some evidence that the colony on Bishop and Clark has increased since the 1960's. Mackenzie (1968) reported that there were 25+ pairs nesting there in the 1960's and Lugg *et al.* (1978) estimated that there were at least 44 pairs nesting on these islets. However, these estimates were obtained from ship-based observations and consequently their accuracy is questionable. The estimate of 140 pairs made by Nigel Brothers was done from the islet itself in March 1992 and the number of eggs laid was estimated from the number of chicks and empty nests.

The number of eggs laid by Black-browed albatrosses increased by 18% between 1994/95 and 1999/00 (2.5 - 4% per annum); however, a decrease of 15% was observed from 1999/00 to 2000/01. This decline was offset by the presence of at least four pairs that exhibited typical pre-laying behaviour, including copulation in 2000/01, but did not lay. Consequently, it is unlikely that the lower number of eggs laid in the 2000/01 season was an indication of a decrease in the breeding population. It is possible that the condition of some Black-browed albatrosses returning after the winter of 2000 was inadequate and as a result egg laying was deferred. A similar condition-dependent deferral of breeding has been observed in other Procellariiforme species (Drent and Daan 1980; Croxall 1991; Chastel *et al.* 1995; Langston and Rohwer 1996). It is likely that any reduction in over-wintering body condition of this nature is linked to changes in the available food resources of this species.

3.4.1.1c Grey-headed albatrosses

In a similar manner to Black-browed albatrosses, the number of breeding Grey-headed albatrosses found in the current study were significantly higher than those reported by Copson (1988). Again, this could be due to Copson (1988) underestimating breeding numbers by missing a) early failures, b) breeders that laid later than his census or c) nests that were cryptically located on the steep and often inaccessible slopes. Alternatively, the Grey-headed albatross breeding population may actually have been at significantly lower levels between 1978 and 1985 and increased to its current levels over the last 20 years. Support for the latter

hypothesis was provided by a significant increase in the number of chicks fledged each year in the last seven seasons relative to the number fledged each year between 1978 and 1985; however, the differences between the two studies are too great to draw such conclusions definitively.

There was no consistent trend in breeding numbers of Grey-headed albatrosses since 1994/95 with the number of eggs laid each year being variable and ranging from a high 83 in 1995/96 to a low of 65 in 1999/2000. Although it is more difficult to accurately ascertain total population numbers of biennially breeding species from annual counts, the relative consistency of breeding numbers over the seven year time period suggests that the breeding population is relatively stable. However, such conclusions are only tentatively made in the context of the relatively short time frame of the present study.

3.4.1.1d Light-mantled sooty albatrosses

There is no evidence of any major fluctuations in breeding numbers of Light-mantled sooty albatrosses on Macquarie Island since 1994/95. The dataset used to examine trends in breeding numbers of this species covers a shorter time-frame than that used for the other three species under investigation. In addition, the number of eggs laid was relatively similar at each site between years and there was no significant variation in overall numbers. The time frame of this study into breeding numbers of Light-mantled sooty albatrosses on Macquarie Island is too short to make any definitive conclusions about population trends but at this stage it appears that population numbers are stable.

3.4.2 Survivorship

3.4.2.1 Overall adult and fledgling survivorship

Survivorship of adults and fledglings was estimated for Wandering (1955-2000), Black-browed (1976-2000) and Grey-headed albatrosses (1976-2000). Goodness-of-fit tests (GOF), Akaike's Information Criteria (AICc) and Likelihood Ratio Tests (LRT) were used effectively to ascertain the most parsimonious model that fitted each dataset and the nature of the variation in survivorship and re-capture probability (i.e. time-dependent, age-dependent, constant). Both AICc values and LRT tests were used to test models, as there is still debate as to which is the most appropriate tool for model selection (Lebretton *et al.* 1992; Burnham and Anderson 1998). The use of the two methods in the current study yielded very similar results. No models were fitted to the dataset of Grey-headed albatrosses 'banded as adults' and it is likely there were not enough resights in this dataset to allow simple models to be fitted.

In all cases the best models had time-dependent re-capture probability, indicating that there were different levels of re-sight effort on the ground on Macquarie Island each year. There was no real evidence (on the basis of AICc values and LRT) that adult or fledgling survivorship of Black-browed and Grey-headed albatrosses showed significant inter-annual variation. However, there was strong evidence that survivorship of Wandering albatross fledglings was time-dependent and some evidence that adult survivorship was time-dependent. Adult survivorship calculated using the Wandering albatross 'banded as chicks' dataset was higher than survivorship calculated using the Wandering albatross 'banded as adults' dataset. The lower (and more variable) survivorship calculated from the latter dataset was possibly attributable to birds that were banded as adults becoming more wary of people and subsequently less likely to be resighted. Thus the adult survivorship calculated from the Wandering albatross 'banded as chicks' dataset is probably a more accurate reflection of adult survivorship and therefore this value used in the comparisons with other studies (section 3.4.1.3).

Grey-headed albatrosses had the highest mean survivorship of 96.7±1.1(s.e)%. Wandering albatrosses also had a high mean adult survivorship (95.3 ± 0.6 %) while Black-browed albatrosses had the lowest mean adult survivorship (91.5 ± 1.1 %). This is consistent with Weimerskirch *et al.* (1987) who suggested that survivorship of adult albatrosses was linked to their life-history parameters and that biennially breeding species, including Wandering and Grey-headed albatrosses, tend to have higher survivorship than annually breeding species such as Back-browed albatrosses because of differences in foraging ecology and breeding biology.

A different pattern was observed in the mean fledgling survivorship estimates. Black-browed albatrosses had the highest survival of fledglings to their first resight on land (58.5 ± 5.8 %) followed by Wandering albatrosses (45.9 ± 3.5 %) and Grey-headed albatrosses (33.6 ± 4.6). Prince *et al.* (1994) suggested that differences in fledgling survivorship may be attributable to different at-sea distributions of the younger birds. Although first resights of fledglings of all three species have occurred at five years of age, Grey-headed albatrosses generally spend longer at sea before returning to land and this may account in part for the apparent lower fledgling survivorship. It should also be noted that the mean Wandering albatross fledgling survivorship value is of limited value as LRT test showed that there was significant inter-annual variation.

3.4.2.2 Variation in survivorship of Wandering albatrosses over time

The variation in Wandering albatross survivorship was analysed by calculating annual fledgling survivorship and also using maximum likelihood estimates of survivorship for ten year periods between 1955 and 1995. Using survivorship calculated over ten year periods allowed a clearer picture of broad trends to be established, as due to the small number of chicks fledging each year, annual survivorship often fluctuated significantly between years. Fledgling survivorship reached its lowest point between 1965-1975 (35.9 ± 9.1%) and 1975 - 1985 (42.5 ± 8.3%). Fledgling survivorship was at its highest between 1985 and 1995 (64.4 ± 7.2%). The variation in fledgling survivorship appeared to be most closely related to the number of hooks set in the eastern Indian Ocean (80°E-140°E) and therefore we hypothesise that fledgling Wandering albatrosses were foraging (and interacting with long-line fisheries for tuna) in that region of the Indian Ocean.

Adult survivorship was also calculated using maximum-likelihood estimates over ten-year periods between 1955 and 1995. Very similar estimates were calculated for the decades 1956-1965 and 1966-1975 (92.5 ± 1.0 %, 92.3 ± 2.0 % respectively). Adult survivorship was higher over the next two decades (1976-1985 – 99.5 ± 0.5%, 1986-1995 – 99.2 ± 0.8). There was no apparent relationship between the numbers of hooks set each year in any the oceans and the variation in adult survivorship. It is likely that this variation was linked to elevated mortality levels due to long-line fisheries operations but the spatial scales over which the hook set data were examined were too large to identify any links between the two datasets. Variation in adult survivorship may have been sex-dependent as several studies have shown that females and juveniles are more likely to be caught on tuna long-lines (e.g. Brothers 1991; Brothers *et al.* 1999; Gales *et al.* 1999). There were not enough historical data on the sex of Wandering albatrosses to undertake these analyses in the current study.

3.4.3 Comparisons with other subantarctic populations

3.4.3.1 Trends in breeding numbers

From the 1970's to the beginning of the 1990's, breeding numbers of Wandering albatrosses in the southern Indian Ocean (Iles Crozet, Marion Island) showed a very similar trend to that observed on Macquarie Island (Weimerskirch *et al.* 1998; Nel *et al.* 2002a). At both locations breeding numbers declined through the 1970's and 1980's to reach a minima in the mid-1980's before increasing again through the late 1980's and early 1990's (Weimerskirch *et al.* 1997a; Nel *et al.* 2002a). However, in contrast to the trend on Macquarie Island, Nel *et al.* (2002a) described a significant decrease in breeding numbers on Marion Island between

1997/98 and 1999/00. Breeding numbers of the Amsterdam albatross (*Diomedea amsterdamensis*), a close conspecific of the Wandering albatross breeding in the south-east Indian Ocean, have been monitored since 1983 and population numbers have increased since that time in a manner that closely parallels the increase (both in trend and numbers) observed on Macquarie Island (Weimerskirch *et al.* 1997a; Inchausti and Weimerskirch 2001).

The foraging areas of Wandering albatrosses breeding on Marion Island and Iles Crozet have been documented using satellite telemetry and these studies show a significant amount of overlap with long-line fisheries, particularly those fishing for tuna in the Indian Ocean, (Weimerskirch et al 1997a; Weimerskirch 1998; Nel et al. 2002a). The foraging areas of the Amsterdam albatross also appear to overlap with these areas in the Indian Ocean (H. Weimerskirch unpublished data, cited in Inchausti and Weimerskirch 2001). The declines in Wandering albatross breeding numbers at Marion Island and Iles Crozet were attributed to elevated mortality levels due to interactions with long-line vessels fishing for tuna. Similarly the increases observed at these locations and in the Amsterdam Island were typically associated with a decrease in fishing effort in and changes in the spatial distribution of this effort (Weimerskirch *et al.* 1997a; Weimerskirch *et al.* 1998; Nel *et al.* 2002a). The parallel trends of breeding numbers on Macquarie Island provided evidence (albeit circumstantial) that birds from this population were under similar pressure from long-line fishing vessels fishing for tuna in the Indian Ocean and that the decline and increase in population numbers since the late 1960's is attributable to elevated mortality levels from interactions with these fisheries.

In contrast to the Macquarie Island and Indian Ocean breeding populations, the number of Wandering albatrosses breeding at South Georgia in the Atlantic Ocean showed a different trend, with numbers declining steadily from a high of over 1900 pairs in the early 1960's to below 1300 pairs in 1996 (Croxall *et al.* 1998). As in the studies on the Indian Ocean populations, this decline has been linked to long-line fisheries operating along the Patagonian shelf where birds from this population preferentially forage (Croxall *et al.* 1998; Prince *et al.* 1998; Croxall and Wood 2002). Unlike the Indian Ocean populations, no increase was observed in breeding numbers from South Georgia in the late 1980's and early 1990's and the population has shown a relatively steady decline throughout this time (Croxall *et al.* 1998).

The proliferation of long-liners fishing for Patagonian Toothfish along the Patagonian Shelf (Moreno *et al.* 1996) could also be associated with the continuous decline documented at South Georgia and studies have demonstrated significant overlap of this species with this fishery, particularly during the chick brooding period (Croxall and Prince 1996; Prince *et al.*

1998). Twenty-nine Wandering albatrosses were caught and killed on 14 monitored Patagonian Toothfish vessels fishing over the Patagonian Shelf (Moreno *et al.* 1996) and although this only represented 2% of the total by-catch it is evidence of increased mortality of this species due to this fishery. Wandering albatrosses from the Marion Island population do not appear to be suffering from significant elevated mortality levels due to interactions with this fishery (Nel *et al.* 2002a; Nel *et al.* 2002b; Nel *et al.* 2002c).

Trends in breeding numbers of Black-browed and Grey-headed albatrosses have also been documented at other subantarctic locations. Waugh *et al.* (1999b) described a steep decline in the Campbell albatrosses (*Thalassarche impavida*), a very similar conspecific breeding on Campbell Island from the 1970's to the mid-1980's, following which the population increased slightly at average rates of 1.1 - 2% per annum. These authors also described the Campbell Island Grey-headed albatross breeding population as declining into the 1990's. Croxall *et al.* (1998) suggested that the Black-browed population on Bird Island, South Georgia was stable or slightly increasing between the 1970's and late 1980's, after which it declined sharply by about 30%. These authors also described declines in the Grey-headed breeding population on South Georgia but also noted this population had the highest level of inter-annual variation.

In a similar pattern to the Bird Island population, Weimerskirch *et al.* (1998) described the breeding population of Black-browed albatrosses as stable on Iles Kerguelen between 1979 and 1990, after which the population declined due to a decrease in juvenile recruitment. Few published data on the population trends of Black-browed albatrosses in the Falkland Island are available since the first census of Steeple Jason Island in 1987 (Thompson and Rothery 1991). However, recent data suggests that the Falkland Island populations have declined in the last 20 years with significant decreases occurring in the last five years (BirdLife International 2001b). Nel *et al.* (2002a) documented a decrease in the Grey-headed albatross population on Marion Island during the 1980's followed by an increase at around 3.6 % p.a. in the 1990's.

In all of the above studies, all population declines were linked to elevated mortality levels caused by interactions with long-line fisheries. The stable population trends observed in the Black-browed and Grey-headed breeding populations on Macquarie Island between the late 1970's and the early 1990's are consistent with those observed on Iles Kerguelen and Marion Island. However the declines observed in these populations at Campbell Island over these time frames were not observed on Macquarie Island. Similarly, the decrease in breeding numbers of these two species in the 1990's at Bird Island and Iles Kerguelen were also not observed on Macquarie Island. The foraging areas of the Black-browed and Grey-headed

albatrosses from Macquarie Island are very different from the areas utilised by Indian Ocean and Atlantic Ocean populations (Chapter 7, Prince *et al.* 1998; Weimerskirch 1998) and consequently the impact of long-line fisheries has not been as severe on the Macquarie Island population. Waugh *et al.* (1999b) suggested that the declines in both Black-browed and Grey-headed population numbers on Campbell Island were attributable to long-line fishing in the Australasian region. Although geographically close, these populations still utilise different foraging areas (Chapter 7, Waugh *et al.* 1999a) and again, this may explain the differences in the population trends.

Few published data on trends in breeding numbers of Light-mantled sooty albatrosses at other locations are available. The only comparable data are presented by Weimerskirch *et al.* (1998) who reported a decrease of 1.7 % per annum in the Light-mantled sooty albatross population at Possession Island between 1980 and 1994. Satellite tracking studies have shown that this species forages in pelagic Antarctic waters, mostly along the Antarctic continent (Weimerskirch and Robertson 1994, Weimerskirch 1998). Such areas are targeted by long-liners fishing for Patagonian Toothfish (including illegal, unregulated and unreported fisheries) and therefore it is likely that this population will be increasingly at risk as the extent of these fisheries increases (Brothers *et al.* 1999).

3.4.3.2 Survivorship

Survivorship estimates from Macquarie Island and comparable estimates from other locations are summarised in Table 3.11. Juvenile recruitment has traditionally been used to describe the survivorship of fledglings to recruitment into the breeding population. However, many studies have calculated survivorship of juveniles to five years of age, or first resight and these estimates are directly comparable to the fledgling survivorship calculated as part of the current study.

Mean adult survivorship of Wandering albatrosses on Macquarie Island was slightly higher than survivorship on Bird Island and Iles Crozet, but lower than the similar conspecific Gibson's albatross (*Diomedea gibsoni*) on the Auckland Islands. However, the higher survivorship on the Auckland Islands was calculated over a significantly shorter time period and was much more similar to adult survivorship on Macquarie Island between 1985 and 1995 (99.3 ± 0.7%). There was no evidence that adult survivorship varied significantly between 1976 and 1993 on Bird Island (Croxall *et al.* 1998); however, significantly lower adult survivorship was recorded between 1966 and 1976 relative to 1977-1993 on Iles Crozet (Weimerskirch *et al.* 1997a).

Table 3.11
Comparison of survivorship estimates for Wandering, Black-browed and Grey-headed albatrosses and close conspecifics from four sub-antarctic breeding sites

	Adult survivorship		Fledgling Survivorship		
Location	**Time period**	**Survival ± s.e**	**Time period**	**Survival ± s.e**	**Source**
Wandering albatross (*Diomedea exulans*)					
Macquarie Island	1956-2000	95.3 ± 0.6	1956-1996	45.9 ± 3.5	This study
Bird Island	1976-1993	91.9 - 93.2	1972-1993	48.9 - 52.4	Croxall *et al.* (1998)
Iles Crozet	1966-1995	93.1 ± 1.8	1966-1995	38.2 ± 13.9	Weimerskirch and Jouventin (1998)
Gibson's albatross (*Diomedea gibsoni*)					
Auckland Islands	1993-1995	97.0 ± 2	-	-	Walker and Elliot (1999)
Amsterdam albatross (*Diomedea amsterdamensis*)					
Amsterdam Island	1983-1993	95.7 ± 1.8	1979-1985	70.4 [A]	Weimerskirch *et al*. (1997)
Black-browed albatross (*Thalassarche melanophrys*)					
Macquarie Island	1976-2000	91.5 ± 1.1	1976-1995	58.5 ± 5.8	This study
Bird Island	1976-1993	91.5 ± 4	1977-1986	15.0 - 23.4	Croxall *et al.* (1998)
Iles Kergualen	1979-1995	90.6 ± 0.5	1979-1995	13.7 ± 7.2	Weimerskirch and Jouventin (1998)
Campbell albatross (*Thalassarche impavida*)					
Campbell Island	1984-1996	94.5 ± 0.7	1975-1989	28.6 ± 0.9	Waugh *et al.* (1999)
Grey- headed albatross *(Thalassarche chrysostoma)*					
Macquarie Island	1976-2000	97.2 ± 1.2	1976-1993	30.8 ± 4.4	This study
Bird Island	1977-1993	93.4 ± 2	1976-1986	18.6 - 19.1	Croxall *et al.* (1998)
Campbell Island	1984-1996	95.3 ± 0.9	1975-1989	23.5 ± 2.0	Waugh *et al.* (1999)

[A] - overall survival of fledglings from 1979-1983

The magnitude and time frame of the variation on Iles Crozet is very similar to that observed in adult survivorship on Macquarie Island, although the survivorship between 1976 and 1995 was higher on Macquarie Island (99 % cf 94-96 %). Mean adult survivorship on Macquarie Island (1955-2000) was also very similar to mean adult survivorship on Amsterdam Island (1983-1993 - Weimerskirch *et al.* 1997a); however, during 1986-1995 adult survivorship on Macquarie Island was considerably higher. Mean fledgling survivorship of Wandering albatrosses on Macquarie Island was similar to that observed on Bird Island and Iles Crozet. Similarly to Macquarie Island, fledgling survivorship at Iles Crozet was lowest between 1965 and 1975 and gradually increased from 1975 to 1985 (Weimerskirch *et al.* 1997a). However, the survivorship of fledgling Wandering albatrosses at Bird Island did not differ significantly between cohorts fledging from 1972-1975 (48.9%) to 1979-1989 (52.4%) and most variation in survivorship occurred between the first resight of a returning fledgling and its recruitment into the breeding population (Croxall *et al.* 1998).

The overall adult survivorship of Black-browed albatrosses (including *T. impavida*) was similar across all locations and despite some significant inter-annual fluctuations; no significant time-dependent trends were identified (Croxall *et al.* 1998; Weimerskirch *et al.* 1998; Waugh *et al.* 1999b). Fledgling survivorship of Black-browed albatrosses from Macquarie Island was at least twice as high as estimates reported at Campbell Island (*T. impavida*), Bird Island and Iles Kerguelen. Such differences are likely to be due to different foraging grounds and different levels of interaction with long-line fisheries (see Section 3.4.4). Fledgling survivorship of Black-browed albatrosses decreased significantly from 23.4% between 1976 and 1981 to 15.0% from 1982-1986 at Bird Island (Croxall *et al.* 1998) and was cited as the main cause of the decline in breeding numbers (Prince *et al.* 1994). Adult survivorship of Grey-headed albatrosses on Macquarie Island was higher than that reported on Campbell Island and Bird Island and no significant time-dependent variation was found at either location. Although recruitment of juvenile Grey-headed albatrosses into the breeding population decreased dramatically at Bird Island from 1976-1982 (8.3 %) relative to 1982-1986 (3.3 %), fledgling survivorship was consistent at 19 % over these two time periods (Croxall *et al.* 1998). Fledgling survivorship of Grey-headed albatrosses at Macquarie Island was most similar to that found on Campbell Island.

3.4.4 Long-line fishing and its impact on breeding numbers and survivorship

3.4.4.1 Wandering albatrosses

Inferential and circumstantial evidence has been presented to suggest that elevated mortality levels from interactions with long-line fisheries have significantly affected breeding numbers

of Wandering albatrosses on Macquarie Island. This is indicated by both the variation in the number of eggs laid each year and the variation in adult and fledgling survivorship. de la Mare and Kerry (1994) also documented this decline in breeding numbers and linked it to long-line fishing activities. These authors fitted a simple model that estimated the survivorship of adults birds that were already banded, and assumed that there was constant re-capture probability between years. They concluded that the decrease in the Macquarie Island breeding population was largely attributable to a decrease in adult survivorship from 97.1 % to 87.1 % as the long-line fishery developed through the 1960's and 1970's. By re-constructing the Wandering albatross database, fitting more complex models that allowed juvenile and adult survivorship to be examined independently, and allowing for time-dependent re-capture probability, different estimates of survivorship and conclusions were reached in the current study. The higher adult survivorship estimated in the current study is attributable to the independent calculation of juvenile survivorship.

Fledgling survivorship of Wandering albatrosses on Macquarie Island varied significantly with time between 1956 and 1995, declining sharply with the onset of the long-line tuna fishery in the early 1960's and continuing to remain well below 40% in most years between 1965 and 1982. Therefore very few juvenile birds were being recruited into the breeding population during this time period (and throughout the 1980's) and this is likely to have been a fundamental mechanism behind the population decline in the late 1960's and 1970's and the slow recovery observed in the late 1980's. Juvenile recruitment started to increase in the early-mid 1980's, which coincided with the population increase in the late 1980's and early 1990's. Although it was an important factor, it is unlikely that variation in fledgling recruitment was solely responsible for the rapid decline and increase in breeding numbers (e.g. see Croxall *et al.* 1998). Adult survivorship also increased from approximately 92% between 1955 and 1975 to approximately 99 % between 1975 and 1995. In conjunction with the increase in fledgling survivorship, this meant that breeding birds already recruited into the breeding population were much more likely to return and continue to breed in subsequent years.

The variation in fledgling survivorship was most closely associated with long-line fisheries operations in the eastern half of the Indian Ocean and periods of increased fishing effort correlated with low fledgling survivorship. Fledgling Wandering albatrosses may be more at risk from long-line operations because they forage almost exclusively in pelagic waters, and rarely venture into feeding grounds closer to land (Weimerskirch and Jouventin 1987). It is also possible that young, naïve birds are caught more frequently as by-catch on fishing vessels (Brothers 1991; Moloney *et al.* 1994). There was no clear statistical correlation with the

variation in adult survivorship and number of hooks set in any of the ocean subsets examined. However, a similar lack of correlation was found in adult survivorship of Wandering albatrosses from Iles Crozet and fishing effort around the Crozet region (Weimerskirch *et al.* 1997a; Weimerskirch *et al.* 1998) and it is likely that the range of the Wandering albatrosses throughout the different stages of the breeding cycle (e.g. see Jouventin and Weimerskirch 1990, Prince *et al.* 1998; Weimerskirch 1998) precludes the identification of any relationship with number of hooks set in a discrete spatial area.

Several complex models (all based on the typical Leslie matrix model - Caswell 1989) have been created in an attempt to better explain or predict the results of interactions between long-line fishing operations and trends in breeding numbers of Wandering albatrosses (e.g. Moloney *et al.* 1994; Weimerskirch *et al.* 1997; Tuck *et al.* 2001). In the most recent attempt, (Tuck *et al.* 2001) was able to predict reasonably closely the observed data from Crozet Islands but was unable to successfully predict the observed data from the South Georgian population. These authors suggested that the reason for the poor fit of the model to the South Georgia data was due to a) less overlap between the Wandering albatross foraging ranges and long-line fishing and b) a lack of reliable data on long-line fishing effort, particularly in relation to illegal, unreported or unregulated (IUU) fishing vessels. Both of these issues are relevant when trying to clarify the interactions between Wandering albatrosses from Macquarie Island and long-line fisheries. The only way that we will further elucidate the effect of long-line fishing on Wandering albatrosses from Macquarie Island (both historically and in the future) is to a) continue to monitor breeding numbers on the ground, b) identify the foraging areas of this species and c) continue to advocate greater observer effort and identification (and mitigation) of IUU fishing operations.

3.4.4.2 Black-browed, Grey-headed and Light-mantled sooty albatrosses

It is possible that breeding numbers declined prior to the late 1970's before the first detailed study into population numbers was conducted (Copson 1988), and there is some evidence for this from the small decline of the Black-browed population breeding in the north of Macquarie Island between 1950 and 1980. The evidence presented here suggests that the impact of long-line fishing on the Black-browed and Grey-headed breeding populations at Macquarie Island has not been significant since the late 1970's. The number of pairs breeding each year since 1994/95 was higher than that recorded in the late 1970's and early 1980's and there is no evidence that adult or juvenile survivorship underwent significant fluctuations since this time. This is in direct contrast to Campbell Island where Waugh *et al.* (1999b) documented the decline of both the Grey-headed and Campbell albatrosses through the

1970's and 1980's and suggested that elevated mortality from long-line fishing was at least partly responsible. The different population trends in the geographically close populations may be due to the different foraging areas that they utilise and this aspect is addressed in more detail in Chapter 7.

Elevated mortality of Black-browed albatrosses and Grey-headed albatrosses breeding at Iles Kerguelen and Bird Island have also been directly linked to interactions with long-line vessels, particularly those fishing for Patagonian Toothfish (Croxall *et al.* 1998; Weimerskirch *et al.* 1998; Cherel *et al.* 1996; Weimerskirch *et al.* 2000b). The Patagonian Toothfish Industry is increasing each year and long-liners searching for this fish are expanding their range, both legally and illegally (Brothers *et al.* 1999; SC-CCAMLR XIX 2000; Lack and Sant 2001; Tuck and Bulman 2001; Nel *et al.* 2002b). Ultimately, this results in more hooks being set each year and due to the unregulated nature of much of the industry; many of these vessels are unlikely to employ mitigation measures, and bycatch is likely to be a major issue (Nel *et al.* 2002c, SC-CCAMLR XIX 2000; SC-CCAMLR XX 2001). The only way in which the impacts of such vessels on breeding populations can be identified and quantified is by long-term monitoring of population demographics at the breeding grounds of the species at risk.

Appendix 3.1a Models fitted to Wandering albatross data (banded as chicks subset)

Model	AICc	Delta AICc	AICc Wt.	# Par	Deviance
Φ{fl(t) ad(.)} p(t)	2342.51	0.00	0.84	89	1583.68
Φ{fl(.) ad(.)} p(t)	2345.86	3.35	0.16	50	1681.62
Φ{(fl(t) ad(t)} p(t)	2388.60	46.09	0.00	124	1535.07
Φ{fl(t) ad(.)} p(.)	2727.29	384.78	0.00	44	2076.69
Φ{fl(.) ad(.)} p(.)	2734.90	392.92	0.00	3	2169.80
Φ{(fl(t) ad(t)} p(.)	2754.75	412.23	0.00	88	1998.47

Appendix 3.1b Models fitted to Black-browed albatross data (banded as chicks subset)

Model	AICc	Delta AICc	AICc Wt	# Par	Deviance
Φ{fl(.) ad(.)} p(t)	1267.36	0.00	0.97	17	620.07
Φ{fl(t) ad(.)} p(t)	1276.03	8.67	0.01	27	607.07
Φ{(fl(t) ad(t)} p(t)	1278.95	11.60	0.00	38	585.22
Φ{(fl(t) ad(t)} p(.)	1783.41	516.06	0.00	24	1121.04
Φ{fl(.) ad(.)} p(.)	1790.24	522.88	0.00	3	1172.01
Φ{fl(t) ad(.)} p(.)	1795.75	528.39	0.00	20	1142.04

Appendix 3.1c Models fitted to Grey-headed albatross data (banded as chicks subset)

Model	AICc	Delta AICc	AICc Wt	# Par	Deviance
Φ{fl(.) ad(.)} p(t)	1479.74	0.00	0.97	27	631.72
Φ{fl(t) ad(.)} p(t)	1486.96	7.22	0.03	45	598.54
Φ{(fl(t) ad(t)} p(t)	1514.26	34.52	0.00	58	595.15
Φ{fl(.) ad(.)} p(.)	1817.32	337.58	0.00	3	1017.65
Φ{fl(t) ad(.)} p(.)	1823.91	344.17	0.00	21	988.84
Φ{(fl(t) ad(t)} p(.)	1871.41	391.67	0.00	44	985.30

Appendix 3.1d Models fitted to Wandering albatross data (banded as adults subset)

Model	AICc	Delta AICc	AICc Wt	# Par	Deviance
Φ{1stR(t) 2ndR(.)} p(t)	2444.144	0	0.99974	44	1650.9
Φ{1stR(t) 2ndR(t)} p(t)	2460.655	16.51	0.00026	70	1606.25
Φ(.) p(t)	2477.469	33.33	0	42	1688.74
Φ{1stR(.) 2ndR(t)} p(t)	2492.676	48.53	0	68	1643.143
Φ{1stR(.) 2ndR(.)} p(t)	2497.837	53.69	0	44	1704.592
Φ(t) p(t)	2498.157	54.01	0	70	1643.752
Φ{1stR(.) 2ndR(.)} p(.)	2573.961	129.82	0	3	1868.381
Φ(.) p(.)	2575.402	131.26	0	2	1871.838
Φ(t) p(.)	2613.189	169.05	0	47	1813.122

Appendix 3.1e Models fitted to Black-browed albatross data (banded as adults subset)

Model	AICc	Delta AICc	AICc Wt	# Par	Deviance
Φ{1stR(t) 2ndR(.)} p(t)	942.57	0.00	0.45	29	320.14
Φ(.) p(t)	942.75	0.18	0.41	22	335.99
Φ{1stR(.) 2ndR(.)} p(t)	944.95	2.38	0.14	23	335.98
Φ{1stR(.) 2ndR(t)} p(t)	954.67	12.10	0.00	35	318.40
Φ{1stR(t) 2ndR(t)} p(t)	955.93	13.36	0.00	41	305.45
Φ(t) p(t)	962.17	19.60	0.00	36	323.56
Φ(t) p(.)	1294.94	352.37	0.00	17	699.08
Φ(.) p(.)	1310.29	367.72	0.00	2	745.75
Φ{1stR(.) 2ndR(.)} p(.)	1311.10	368.53	0.00	3	744.54

Appendix 3.2a Likelihood ratio tests between models, Wandering albatross (chicks only subset)

General Model	# Par.	Reduced Model	# Par.	χ^2	df	Prob.	Notes
Φ{(fl(.) ad( )} p(t)	50	Φ{(fl(.) ad(.)} p(.)	3	488.157	47	< 0.0001	strong evidence that resight probability is time-dependent
Φ{(fl(t) ad(t)} p(t)	124	Φ{fl(t) ad(.)} p(t)	89	48.613	35	0.0628	little evidence that adult survivorship is time dependent
Φ{fl(t) ad( )} p(t)*	89	Φ{fl( ) ad( )} p(t)	50	97.941	39	< 0.0001	strong evidence that juvenile survival is time dependent

Appendix 3.2b Likelihood ratio tests between models, Black-browed albatross (banded as chicks only subset)

General Model	# Par.	Reduced Model	# Par.	χ^2	df	Prob.	Notes
Φ{(fl(.) ad( )} p(t)	17	Φ{(fl(.) ad(.)} p(.)	3	551.945	14	< 0.0001	strong evidence that resight probability is time-dependent
Φ{(fl(t) ad(t)} p(t)	38	Φ{fl(t) ad(.)} p(t)	27	21.855	11	0.0255	evidence that adult survivorship is time-dependent
Φ{fl(t) ad(.)} p(t)	27	Φ{fl(.) ad( )} p(t)	17	12.998	10	0.2238	no evidence that juvenile survival is time-dependent

Appendix 3.2c Likelihood ratio tests between models, Grey headed albatross (banded as chicks only subset)

General Model	# Par.	Reduced Model	# Par.	χ^2	df	Prob.	Notes
Φ{(fl(.) ad(.)} p(t)	27	Φ{(fl( ) ad(.)} p( )	3	385.931	24	< 0.0001	strong evidence that resight probability is time-dependent
Φ{(fl(t) ad(t)} p(t)	58	Φ{fl(t) ad( )} p(t)	45	3.388	13	0.9961	no evidence that adult survivorship varies over time
Φ{fl(t) ad(.)} p(t)	45	Φ{fl(.) ad(.)} p(t)	27	33.176	18	0.0159	evidence that juvenile survival varies over time

Appendix 3.2d Likelihood ratio tests between models, Wandering albatross (banded as adults only subset)

General Model	# Par.	Reduced Model	# Par.	χ^2	df	p-value	Notes
Φ(t) p(t)	70	Φ(t) p(.)	47	169.37	23	< 0.0001	strong evidence that annual resight probability is time dependent
Φ(t) p(t)	70	Φ(.) p(t)	42	44.988	28	0.0221	evidence that annual survival rate varies with time
Φ{1stR(.) 2ndR(.)} p(.)	3	Φ(.) p(.)	2	3.457	1	0.063	little evidence of significant differences between survival to the first resight and subsequent resights
Φ{1stR(t) 2ndR(t)} p(t)	70	Φ{1stR(t) 2ndR(.)} p(t)	44	44.65	26	0.0129	evidence of time-dependent survivorship after the 1st resight
Φ{1stR(t) 2ndR(t)} p(t)	70	Φ{1stR(.) 2ndR(t)} p(t)	68	36.89	2.00	< 0.0001	strong evidence of time dependent survivorship to 1st resight

Appendix 3.2e Likelihood ratio tests between models, Black-browed albatross (banded as adults only subset)

General Model	# Par.	Reduced Model	# Par.	χ^2	df	p-value	Notes
Φ(t) p(t)	36	Φ(t) p(.)	17	375.524	19	< 0.0001	strong evidence that annual resight probability varied over time
Φ(t) p(t)	36	Φ( ) p(t)	22	12.429	14	0.5719	no evidence that overall survival rate was time-dependent
Φ{1stR(.) 2ndR( )} p(t)	23	Φ(.) p(t)	22	0.005	1	0.9436	no evidence that there was any significant difference between survival to the first resight and subsequent resights
Φ{1stR(t) 2ndR(t)} p(t)	41	Φ{1stR(t) 2ndR(.)} p(t)	29	14.689	12	0.2589	no evidence of time dependent survivorship after 1st resight
Φ{1stR(t) 2ndR(t)} p(t)	41	Φ{1stR(.) 2ndR(t)} p(t)	35	12.952	6	0.0438	evidence of time-dependent survivorship to 1st resight

Chapter 4 - Trends in breeding success and individual breeder quality of the albatrosses on Macquarie Island

4.1 INTRODUCTION

The investigation of breeding success (number of chicks fledged from number of eggs laid) and productivity is a critical aspect of any study of population demographics and breeding biology (e.g. Weimerskirch and Jouventin 1987, Croxall 1998). Members of the Procellariiformes, such as albatrosses, lay a single egg (Lack 1968) and due to the prolonged incubation and chick rearing period, annual breeding success in this family is often low (Warham 1990). Overall breeding success is comprised of two components, hatching success (the proportion of chicks hatched from eggs laid) and chick success (the proportion of chicks fledged from eggs hatched).

Many factors influence the failure of a breeding pair to raise and fledge a chick successfully, the most common in Procellariiformes include: infertility, unsuccessful fertilisation of the female, egg abandonment, egg damage, deterioration of nest site or poor nest bowl, injury to the chick, starvation of the chick due to insufficient food supply, plastic ingestion by the chick, predation of the unattended chick and the chick leaving the nest before it is ready to fledge (either voluntarily or involuntarily). Underlying these causal factors are broader aspects including survivorship, the age or experience of breeding birds, mate fidelity, site fidelity, variations in oceanic food resources, weather patterns (both local and global) and the condition of the breeders. Studies have also shown that some individuals in a breeding population have a considerably higher lifetime reproductive output than others (e.g. see reviews in Clutton-Brock 1988) and parental 'quality' is also likely to influence trends in breeding success of albatrosses (Cobley *et al.* 1998).

In pelagic seabirds breeding failure is more common during incubation than during chick rearing (e.g. Prince *et al.* 1994). Egg abandonment is a common cause of failure in many species of albatrosses and tends to occur earlier in incubation when minimal investment has been incurred (Warham 1990). The most common cause of abandonment is the failure of a bird to return from a foraging trip in time to relieve its increasingly hungry mate. The mechanisms behind a breeding bird undertaking longer foraging trips are complex, and likely to include aspects such as foraging efficiency, prey abundance or availability, environmental conditions and the presence/absence of fishing vessels. The ability of albatrosses to remain on the egg over extended periods of time is related to the strength of the pair and egg bonds and

the amount of energy reserves available to the incubating bird (e.g. Croxall 1982; Croxall and Ricketts 1983).

Larger species like the Wandering albatross, with high energy reserves and a strong nest/pair bond, can incubate an egg for up to 50 days before abandoning (Weimerskirch 1995). Smaller species, such as Black-browed, Grey-headed and Light-mantled sooty albatrosses, that do not have access to such reserves of stored energy, have a limited ability to incubate for extended periods (Prince *et al.* 1981). Nevertheless, single shifts of between 20-30 days have been recorded in these species (Tickell and Pinder 1975; Thomas et al. 1983, Chapter 6), suggesting that the ability to incubate for long periods in a single setting is not solely attributable to size.

The breeding success of Wandering albatrosses (*Diomedea exulans*) has been documented at several locations including Bird Island (Croxall *et al.* 1990; Croxall *et al.* 1992; Croxall *et al.* 1998), Possession Island (Weimerskirch *et al.* 1986; Weimerskirch 1992a; Weimerskirch *et al.* 1998), Auckland Islands (*D. gibsoni*) (Walker and Elliott 1999) and Amsterdam Island (*D. amsterdamensis*) (Weimerskirch *et al.* 1997a). Trends in breeding success of Black-browed and Grey-headed albatrosses have also been documented at Bird Island (Tickell and Pinder 1975; Prince *et al.* 1994; Croxall *et al.* 1998), Iles Crozet (Weimerskirch *et al.* 1986; Weimerskirch *et al.* 1998) and Campbell Island (*T. impavida*)(Waugh *et al.* 1999b). Breeding success of Light-mantled sooty albatrosses has been described at Bird Island (Thomas *et al.* 1983), Marion Island (Berruti 1979) and Iles Crozet (Weimerskirch *et al.* 1986; Jouventin and Weimerskirch 1988; Weimerskirch *et al.* 1998). Many of the above studies monitored breeding success of a colony for several years and attributed most of the inter-annual variation in breeding success to fluctuations in oceanic food resources.

Albatrosses forage primarily on squid, pelagic fish and krill (Cherel and Klages 1998) and the distribution of these prey items is influenced by physical and biological processes in the oceans. These processes initially determine the distribution of smaller organisms such as plankton and nekton (Piontkovski *et al.* 1995; Pakhomov and Froneman 1999), which consequently influences the distribution of seabirds and marine mammals (Pakhomov and McQuaid 1996; Perissinotto *et al.* 2000). Due to the patchy distribution of these prey items, little is known about the specific mechanism underlying and determining their distribution (e.g. Cherel and Weimerskirch 1995); however, several studies have demonstrated that they are likely to be associated with the surrounding oceanography (Prince *et al.* 1994; Veit *et al.* 1997; Guinet *et al.* 1998; Waugh *et al.* 1999a; Nel *et al.* 2001; Reid and Croxall 2001; Thompson and Ollason 2001). Examination of fluctuations in oceanographic data (such as

chlorophyll A levels, sea surface temperatures and sea surface height anomalies) may therefore provide insight into the variation in rates of breeding success.

There have been several studies on breeding success of albatrosses on Macquarie Island. Breeding success in Wandering albatrosses was documented from 1965 to 1968 (Carrick and Ingham 1970) and again in more detail between 1974 and 1978 (Tomkins 1985b). Copson (1988) described breeding success of Black-browed and Grey-headed albatrosses between 1978 and 1985, but as discussed in Chapter 3, breeding numbers may have been underestimated in this study and therefore breeding success may be overestimated. Banding of breeding Light-mantled sooty albatrosses was conducted in the north of the island through the 1970's and 1980's and breeding success was calculated over this time period (Kerry and Garland 1984).

Although many studies have documented broad trends in breeding success of albatross colonies or populations, few have tracked the success of individual breeders over time. In a review of reproductive success of contrasting breeding systems, Clutton-Brock (1988) suggested that longitudinal studies that compare the breeding success of the same individuals over time are superior to those that do not. The comprehensively banded populations of Wandering, Black-browed and Grey-headed albatrosses on Macquarie Island represent a unique opportunity to achieve this with entire breeding populations. Studies on Kittiwake gulls (*Rissa trydactyla*) (Coulson and Porter 1985; Thomas and Coulson 1988) and Atlantic fulmars (*Fulmarus glacialis*) (Ollason and Dunnett 1988) showed that individual quality might be one of the more important factors influencing reproductive success. In a study on Wandering albatrosses of known age and experience, Croxall *et al.* (1992) suggested that 'quality' of individual females was a significant factor in the size of the egg laid (and consequently hatching success). Cobley *et al.* (1998) described the individual breeding quality of Grey-headed albatrosses breeding at South Georgia between 1993 and 1995 (based on two decades of breeding data see Prince *et al.* 1994).

In the present study individual breeding birds of all species were monitored over a period of at least three breeding attempts (four for the annually breeding Black-browed albatrosses) and individuals were classified as *top*, *medium* or *bottom* quality breeders. These classifications are also utilised in later chapters to clarify the influence of breeding quality on breeding frequency and attendance patterns.

Diminished breeding success is likely to have serious implications for the long-term viability of albatross populations, particularly those that are small and vulnerable. The data on

breeding success collected here since 1994/95 complement existing data on albatross populations at other subantarctic regions and forms an integral part of the current study into the population dynamics of the albatrosses on Macquarie Island.

4.1.2 Summary of research questions

1. Are there any temporal trends in the breeding success of albatrosses on Macquarie Island and are these trends correlated between species ?

2. Is inter-annual variation on Macquarie Island associated with inter-annual variation in the local oceanography in the foraging areas of these species ?

3. What other factors are likely to impact on breeding success of albatrosses on Macquarie Island ?

4.2 DATA PROCESSING AND ANALYSES

4.2.1 Trends in breeding success

Rates of hatching success, chick success and overall breeding success were calculated using data obtained from daily observations of breeding Wandering, Black-browed and Grey-headed albatrosses (Sections 2.21, 2.2.2, 2,2,3). Annual breeding success of Light-mantled sooty albatrosses was calculated by pooling data from five to nine study sites, and the breeding success at each site was also calculated (Section 2.2.3, Figure 2.4). Therefore, only temporal trends were investigated for the first three species and both spatial and temporal trends of Light-mantled sooty albatross breeding success were examined. Breeding success was calculated for the entire breeding populations of the former three species and a sub-sample comprising approximately 15-25% of the breeding Light-mantled sooty albatrosses (based on an estimate of 1000-1100 pairs breeding each year).

Spearman Rank Correlation Tests (r^s) were initially used in preference to Pearson correlation (r^p, r^2) tests due to the small sample sizes and non-normal distribution of most of the data being analysed (Zar 1974). Pearson Correlation Tests and r^2 values were used to assess any linear relationships that were identified. In the case of multiple comparisons, the False discovery method (Benjamini and Hochberg 1995; Curran-Everett 2000) was used to adjust the significance level and p-values were assessed accordingly.

4.2.2 Oceanographic data

Oceanographic data (chlorophyll A levels, sea surface temperatures and sea surface height anomalies) were obtained for an area bounded by latitudes –45°S and –68°S and longitudes 145°E and 195°E. These boundaries encapsulated the Macquarie Island region and included most of the known foraging areas of Black-browed and Grey-headed albatrosses breeding on Macquarie Island (Chapter 7). These oceanographic data were chosen as they were accessible in dated electronic files (see websites below), and when used together, formed a relatively comprehensive picture of the oceanic environment around Macquarie Island.

1) Sea Surface Temperature - http://podaac.jpl.nasa.gov/mcsst/

The Multi-Channel Sea Surface Temperature (MCSST) data are derived from the 5-channel Advanced Very High Resolution Radiometers (AVHRR) on board the National Oceanic and Atmospheric Administration (NOAA) -7, -9. -11 and -14 polar orbiting satellites. Weekly averaged data for both the ascending pass (daytime) and descending pass (night-time) are provided on an equal-angle grid of 2048 pixels longitude by 1024 pixels latitude (nominally referred to as **18 km** resolution). Data are provided in Hierarchical Data Format (HDF) and in Raw Binary Format (description obtained from above website; Copyright © 1999-2001 NASA/JPL PO.DAAC

2) Chlorophyll A levels - http://seawifs.gsfc.nasa.gov/SEAWIFS.html

Data obtained are level-3 standard mapped images. The level 3 data from the Sea-Viewing Wide Field of View Sensor (SeaWIFS) are statistical data sets derived from level-2 data (level 2 data is at the pixel level-not spatially or temporally averaged). Each level-3 data set is based on a fixed global grid of equal area bins that are approximately 9 km by 9 km (Campbell *et al.* 1995). Note: Data provided by the SeaWiFS Project, NASA/Goddard Space Flight Centre and ORBIMAGE. All SeaWiFS images and data presented on the above website are for research and educational use only.

3) Sea Surface Height Anomaly (SSHA)

http://www-ccar.colorado.edu/~realtime/global_data_ssh/ssh.html

Data on sea-surface height were obtained using the Global Near Real-Time Altimeter Data Host Program, sponsored by the Colorado Centre for Astrodynamics Research (CCAR) at the University of Colorado, Boulder. This program generates a data file of sea surface heights in any region of the world. The generated data files are sent directly to the web in ASCII format and can be downloaded. Data are in the form of weekly satellite derived TOPEX/Poseidon sea surface height anomaly data. The TOPEX/Poseidon satellite launched in August 1992 was

expected to operate through September 1998. No sea surface height anomaly data prior to 1996 were available. The satellite is currently in operation and measures the global ocean topography every ten days. These data represent a statistical measure of sea-surface height fluctuations from the mean sea-surface level and are indicative of temporal variations in major current systems. (Copyright © 1999-2001 California Institute of Technology. (NASA/JPL PO.DAAC).

Once downloaded the raw data files were converted into text files compatible with ArcInfo 8.0 and ArcView 3.2 (Esri, Redlands, California). These conversions were achieved using filtering programs written in IDL Version 5.2.1 (Interactive Data Language – 1999, Research Systems Inc).

Simple changes in these oceanographic data from around Macquarie Island were quantified and analysed concurrently with the breeding success data and Spearman Rank Correlation Tests were conducted to identify correlations or potential relationships. If these tests yielded a significant result, the values were plotted and r^2 values obtained to quantify the strength of the linear relationship.

4.2.3 Individual breeder quality

The breeding records of individuals were derived from the resight datasets used in Chapter 3 (Section 3.2) prior to the division into chick and adult subsets. Only data obtained in the current study (i.e. 1994/95-2000/01) were used. The success of each breeder was recorded for each year and the timing of each failure was also noted.

A minimum of three breeding attempts were required to assess the breeding quality of the biennially breeding Wandering, Grey-headed and Light-mantled sooty albatrosses, while at least four breeding attempts were required to classify the breeding quality of Black-browed albatrosses. In all cases breeding birds that successfully fledged a chick on more than two-thirds of their breeding attempts were classified as *top* breeders. *Medium* quality breeding birds were those that were successful in 34% to 65% of their breeding attempts and *bottom* quality breeding birds were those that were successful in less than one-third of their breeding attempts. Due to the smaller sample sizes available in the current study, the classification regime used here was slightly different to that used by Cobley *et al.* (1998); however, the proportion of successful breeding attempts used to quantify breeding quality were similar enough for comparisons to be made between the two studies.

4.3 RESULTS

4.3.1 Overview

The mean annual hatching, chick and overall breeding success of each species from 1994/95-2000/01 are summarised in Table 4.1. Wandering and Grey-headed albatrosses had the highest breeding success followed by Light-mantled sooty albatrosses (the least variable) and Black-browed albatrosses. However, due to the relatively high inter-annual variation, particularly in the Wandering albatrosses, these different were not significant (Kruskal Wallis - $\chi^2_3 = 5.6$, $p>0.1$, n.s). Similarly, no significant inter-species differences were found in hatching success ($\chi^2_2 = 5.2$, $p>0.05$, n.s) or chick success ($\chi^2_2 = 5.8$, $p>0.05$, n.s). Nest checks of Light-mantled sooty albatrosses were too infrequent to ascertain hatching dates and therefore hatching success and chick success were not calculated. Mean chick success was significantly higher than hatching success of the Wandering ($\chi^2_1 = 8.1$, $p=0.04$), Black-browed ($\chi^2_1 = 9.4$, $p=0.02$) and Grey-headed albatrosses ($\chi^2_1 = 4.4$, $p=0.035$).

Table 4.1
Mean annual breeding success of albatrosses on Macquarie Island between 1994/95-2000/01

Species	Success	Mean (%)	s.e (%)	Minimum (%)	Maximum (%)
Wandering albatross (7-15 pairs each year)	hatch	64.4	7.0	30.0	85.7
	chick	93.0	3.4	80.0	100.0
	overall	59.7	6.9	30.0	85.7
Black-browed albatross (37-46 breeding pairs each year)	hatch	54.3	3.2	46.7	68.4
	chick	84.7	3.7	68.4	100.0
	overall	46.1	3.6	33.3	57.5
Grey-headed albatross (65-83 breeding pairs each year)	hatch	68.5	3.1	55.7	79.2
	chick	80.3	3.0	70.0	93.0
	overall	55.3	4.0	43.1	73.6
Light-mantled sooty albatross (152-306 annual breeding pairs used in analyses)	overall	50.8	1.9	42.3	55.7

4.3.2 Temporal trends in inter-annual variation of breeding success

4.3.2.1 Trends within species

The contribution of the variation in hatching success and chick success to the variation in overall breeding success was calculated using the methodology of Brown (1988) (Table 4.2). This method is useful in identifying the period of the breeding cycle that has the most influence on overall breeding success. The covariation term represents the interaction of hatching success and chick success and the contribution that the combination of the two success rates has on overall breeding success.

Table 4.2
Contribution of hatching success, chick success and covariation to variation in overall breeding success of albatrosses on Macquarie Island

Species	Hatch (%)	Chick (%)	Covariation (%)
Wandering albatross	87.6	10.0	2.4
Black-browed albatross	58.8	32.3	8.9
Grey-headed albatross	38.1	27.0	34.9

Most variation in overall breeding success of Wandering albatrosses was attributable to variation in hatching success and this was also reflected by the consistently high chick success of Wandering albatrosses between 1994/95 and 2000/01. In contrast, there was a more equal contribution of hatching and chick success to variation in overall breeding success of Black-browed and Grey-headed albatrosses. This was particularly true of Grey-headed albatrosses, and the relatively high contribution of the interaction between the two success rates to overall breeding success indicates that variation in overall breeding success cannot be easily attributed to success during the incubation or chick rearing stage. The variation in hatching success, chick success and overall breeding success of each species and the number of eggs laid between 1994/95 and 2000/01 is illustrated in Figures 4.1-4.4.

Figure 4.1
Hatching success, chick success and overall breeding success of Wandering albatrosses between 1994/95 and 2000/01

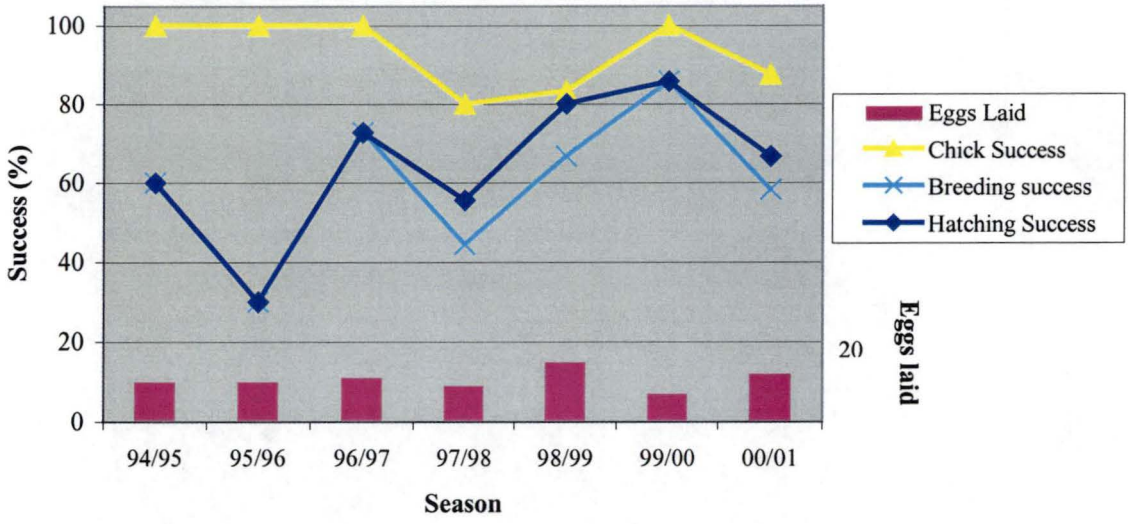


Figure 4.2
Hatching success, chick success and overall breeding success of Black-browed albatrosses between 1994/95 and 2000/01

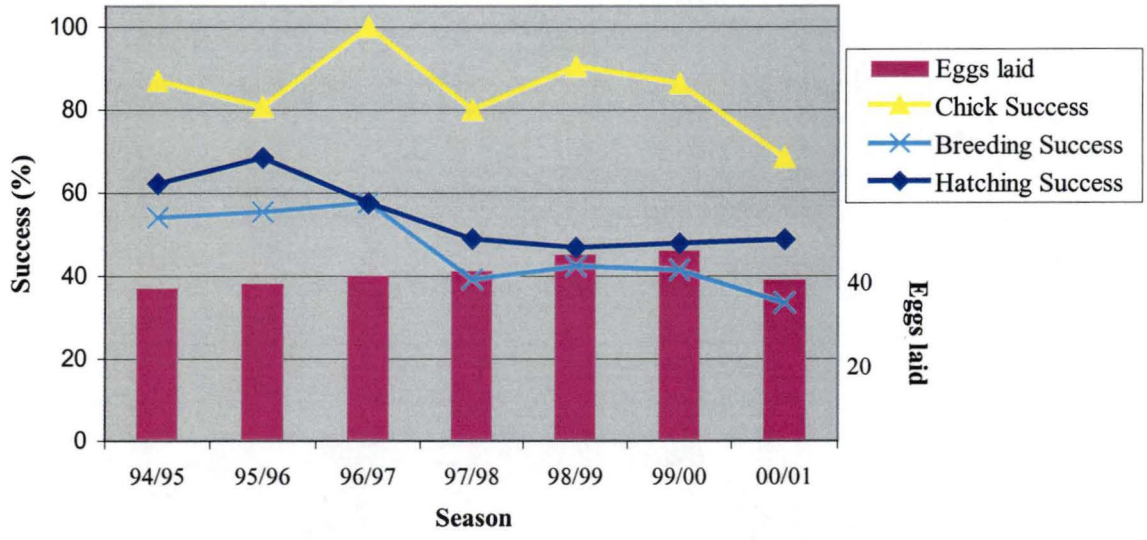


Figure 4.3
Hatching success, chick success and overall breeding success of Grey-headed albatrosses between 1994/95 and 2000/01

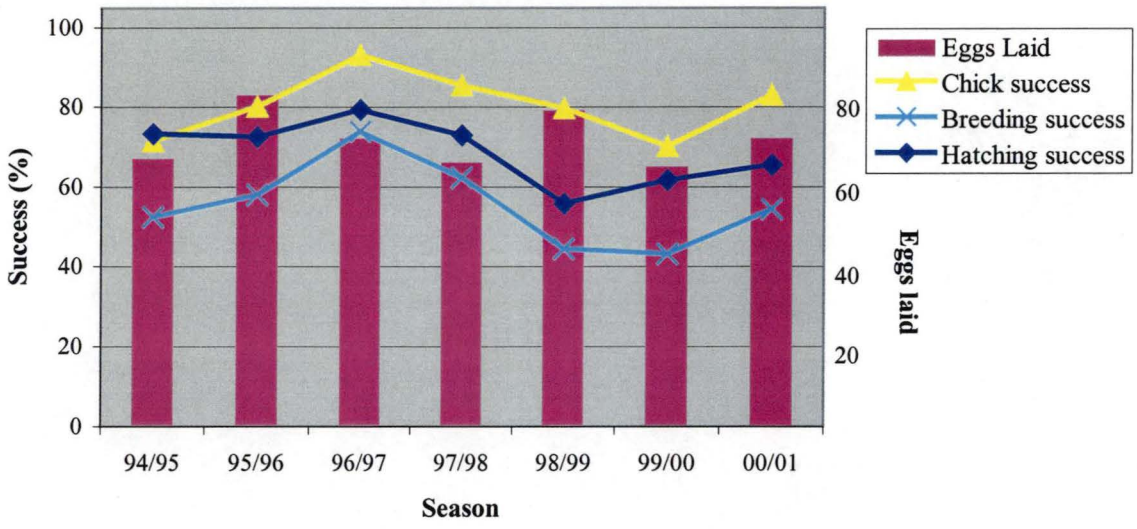
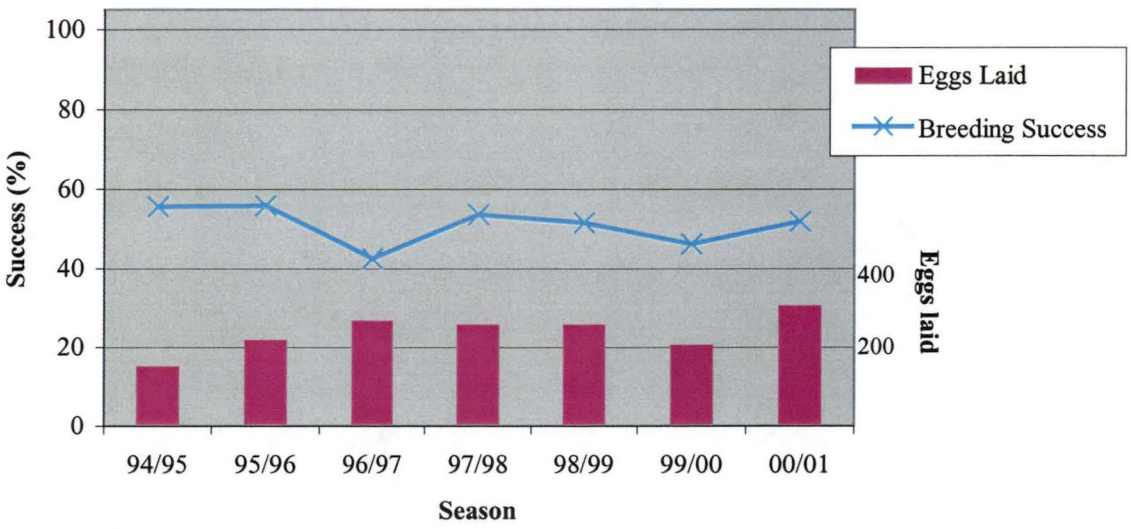


Figure 4.4
Hatching success, chick success and overall breeding success of Light-mantled sooty albatrosses between 1994/95 and 2000/01



Spearman's Rank Correlation Tests were used to further examine the relationship between the three breeding success parameters. Overall breeding success of Wandering albatrosses was positively correlated with hatching success (r^s_7 = 0.93, p=0.001), while overall breeding success of Black-browed albatrosses was positively correlated with chick success (r^s_7 = 0.75, p=0.026). Overall breeding success of Grey-headed albatrosses was positively correlated with both hatching success (r^s_7 = 0.75, p=0.026) and chick success (r^s_7 = 0.93, p=0.001).

4.3.2.2 Between species trends

Despite the marked inter-annual variation shown in Figures 4.1-4.3, the breeding success of Wandering albatrosses showed a general increasing trend between 1994/95 and 2000/01; while the breeding success of Black-browed albatrosses showed a generally decreasing trend over this time period. This inter-species difference was also refected by a significant negative correlation between Wandering albatross hatching success and Black-browed albatross hatching success (r^s_7 = -0.79, p=0.018).

In order to further assess if similar mechanisms were underlying the variation in breeding success of each species, correlation trends were used to compare the variation in breeding success over time. The only significant positive correlation between species was between the hatching success of Black-browed and Grey-headed albatrosses (r^s_7 = 0.75, p=0.026). A significant negative correlation was also found between overall breeding success of Wandering and Light-mantled sooty albatrosses (r^s_7 = -0.86, p=0.007). The overall breeding success of the Light-mantled sooty albatrosses (all sites pooled) showed the least inter-annual variation of all species, which may be a reflection of the larger sample size. However, this lack of temporal variation was also observed at most of the individual Light-mantled sooty study sites for which there are at least six seasons data (Figures 4.5, 4.6). These figures also show that the northern breeding success sites (Gadget and First Gullies, Sandy Bay, Bauer Creek and North Head – see Figure 2.3) tended to have higher breeding success than the southern study sites (Lusitania Bay, Hurd Point, Windsor Bay – see Figure 2.3).

Figure 4.5
Breeding success of Light-mantled sooty albatrosses
at three southern study sites on Macquarie Island (1994/95-2000/01

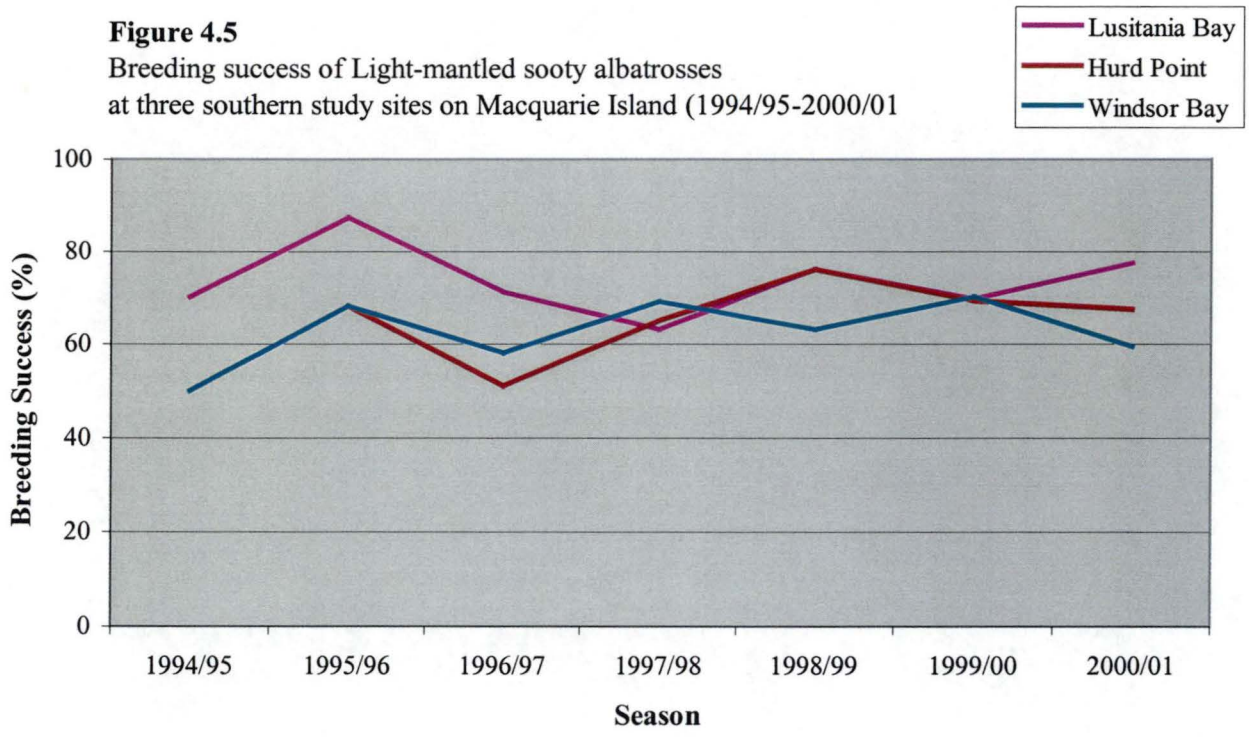
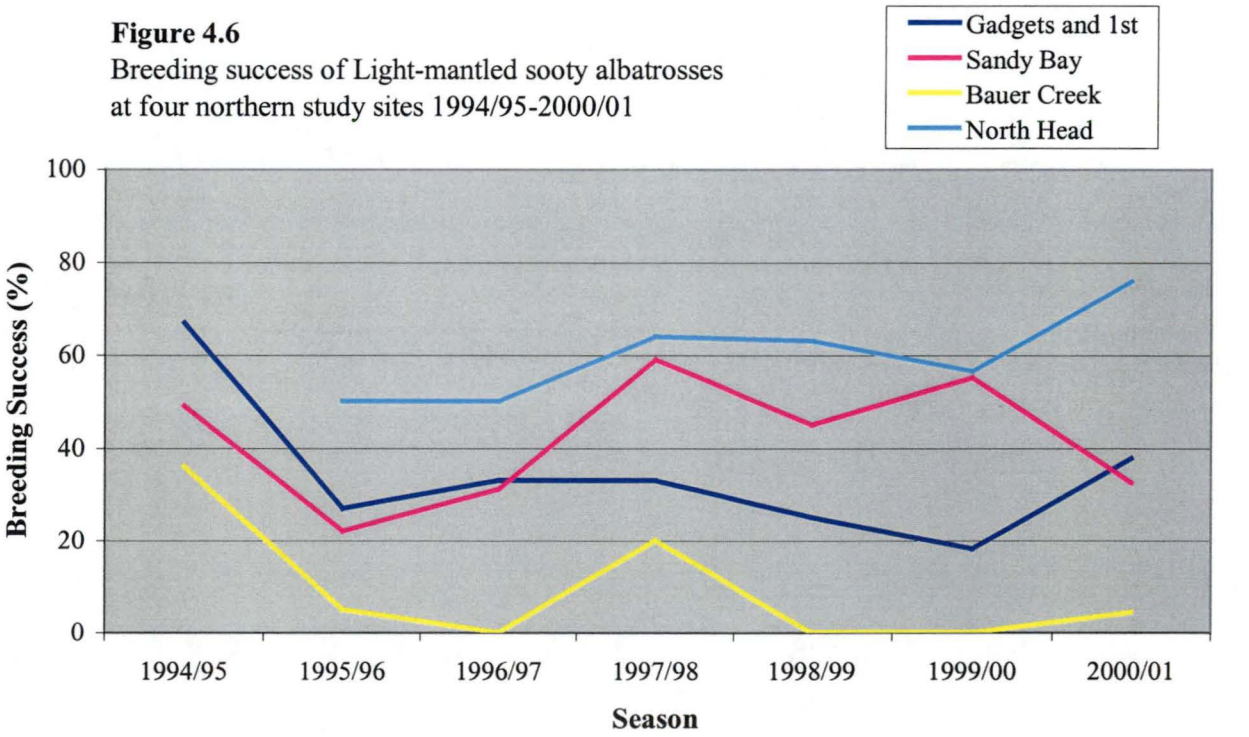


Figure 4.6
Breeding success of Light-mantled sooty albatrosses
at four northern study sites 1994/95-2000/01



4.3.3 Spatial trends in the breeding success of Light-mantled sooty albatrosses

Two-way Analysis of Variance was used to test for temporal and spatial trends in breeding success of the Light-mantled sooty albatrosses. These tests showed that there were no statistical differences between years (Two-way ANOVA, F_6=1.3, ns) but there were significant differences between sites (Two-way ANOVA F_6=23.0, $p<0.001$). Breeding success of sites from the south (Figure 4.5) of Macquarie Island were pooled (mean=59.8±3.) and were significantly higher than the pooled breeding success data from northern study sites (Figure 4.6 - mean=35.0±4.4; t_{49}=-4.2, $p<0.001$).

4.3.4 Research impacts on breeding success.

There was little evidence that our presence had any impact on the breeding success of the Wandering, Black-browed and Grey-headed albatrosses. Of these three species Black-browed albatrosses were the only species to exhibit a decreasing trend from 1994/95 to 2000/01. This decrease could potentially be attributed to our daily presence on the breeding slopes; however, the consistency in overall success from 1994/95 to 1996/97 (~55%) and 1997/98-1999/00 (~41 %) is not the steady decline that might be expected from a negative response to the continual presence of researchers (e.g. Robertson 1998). In addition, there were no daily observations during early incubation in 1999/00 and hatching success in that season was very similar to other seasons where daily observations were conducted throughout incubation.

Of the nine Light-mantled sooty albatross breeding success study sites monitored since 1994/95, two were monitored via remote observations only and another site (North Head) had a relatively high proportion (~30%) of inaccessible nests that could only be remotely monitored. Data on these accessible and inaccessible nests were pooled for each year to test if regular monitoring of nests had any impact on breeding success (Table 4.3).

Breeding success of the inaccessible nests was slightly higher than that observed at the regularly visited accessible nests in six of the seven seasons. Statistical tests (Kruskal-Wallis) showed that this difference was not significant (χ^2_1=2.98, p=0.085); however, the consistently higher success at the inaccessible sites raises the possibility that regular visits may have a net negative impact on breeding success of this species.

Table 4.3
Pooled data of breeding success of accessible and inaccessible nests monitored in the Light-mantled sooty albatross study sites from 1994/95 to 2000/01

	Accessible				Inaccessible			
Season	**# sites**	**# eggs**	**# chicks**	**Breeding success (%)**	**# sites**	**# eggs**	**# chicks**	**Breeding success (%)**
1994/95	5	157	88	56.1	1	37	23	62.2
1995/96	6	145	67	46.2	2	95	68	71.6
1996/97	6	186	76	40.9	2	82	38	46.3
1997/98	7	186	101	54.3	2	72	37	51.4
1998/99	7	184	94	51.1	2	74	38	51.4
1999/00	7	151	67	44.4	2	56	28	50.0
2000/01	7	230	113	49.1	2	76	45	59.2

4.3.5 Trends in breeding success and local fisheries

The Australian Fishery Management Authority (AFMA) has restricted commercial fisheries for Patagonian Toothfish (*Dissostichus eleginoides*) around Macquarie Island to trawling and to a single vessel. Trawling operations began around Macquarie Island in 1994/95. Although all albatross species breeding on Macquarie Island forage close (< 100 km) to Macquarie Island at some stage during their breeding cycle (Chapter 6, Chapter 7), it is the Black-browed albatrosses that forages almost exclusively around the highly productive undersea ridges close to Macquarie Island that are also targeted by the Australian Licensed Commercial Fishing Vessel (Section 7.3.3.1).

The high degree of overlap between the areas targeted by the fishery and the foraging grounds of Black-browed albatrosses may influence the breeding success of this species. Breeding birds on foraging trips are often habitually attracted to fishing vessels (Hyrenbach 1999; Gremillet 2000) as they often represent a source of food. If this influences their normal attendance patterns then it is possible that these fishing activities directly influence breeding success (Chapter 6). In 1994/95, 1995/96 and 1996/97 the Australian Licensed Commercial Fishing Vessel (ALCFV) did not begin fishing around Macquarie Island until late November or early December. The earlier start to trawling operations and the concurrent drop in

breeding success provide circumstantial evidence that the two may be related. In addition, AFMA observers on board the ALCFV during the latter seasons reported regular sightings of breeding Black-browed albatrosses from Macquarie Island (identified by dye markings – AFMA observers personal communication).

4.3.6 Trends in breeding success and surrounding oceanography

Macquarie Island lies in the Polar Frontal Zone, just south of the Subantarctic Front and north of the Polar Front (fronts and zones as defined by Gordon *et al.* 1977; Whitworth 1980; Orsi *et al.* 1995– see Figure 4.7, summer 1993/94).

4.3.6.1 Sea-surface temperature

Sea-surface temperature data (weekly bins, day-time satellite passes only) were averaged for six-month periods from October to March inclusive from1993/94 to 2000/01. These data were averaged using IDL programs, then 'smoothed' using a rolling boxcar procedure (kernel size =10 units). Data were 'smoothed' as satellite coverage was patchy, even when averaged over a six monthly period. Coverage during winter was even patchier and therefore these data were not utilised in the quantitative analyses.

The resultant data are presented in Figure 4.7 and show the annual variation in sea-surface temperature around Macquarie Island. Macquarie Island usually lies in the temperature band 4.2 - 6.9°C; however, the distance to the warmer (6.9 – 9.7° C) or colder (1.4 – 4.2°C) waters changed each year. These distances were quantified using ArcView 3.2 (with Spatial Analyst extension- no projection of view) and are summarised in Table 4.4. Each distance was measured from the south-western corner of Macquarie Island to the closest edge of the colder and warmer temperature band.

Spearman's Rank Correlation Tests were used to test for correlations between these distances and hatching, chick and overall breeding success rates of the four albatross species. A significant negative correlation was found between overall breeding success of Light-mantled sooty albatrosses and distance to the colder waters ($r^s_7 = -0.75$, $p=0.026$). This suggested that breeding success of this species was higher when colder waters were closer to Macquarie Island. However, when these values were plotted the r^2 estimate (0.33), was not significant ($r^p_7=-0.578$, $p=0.09$, ns). There were no significant correlations between breeding success of the other species and distance to the colder or warmer water.

Figure 4.7
Variation in summer sea-surface temperatures (October March) around Macquarie Island from 1993/94 to 2000/01.

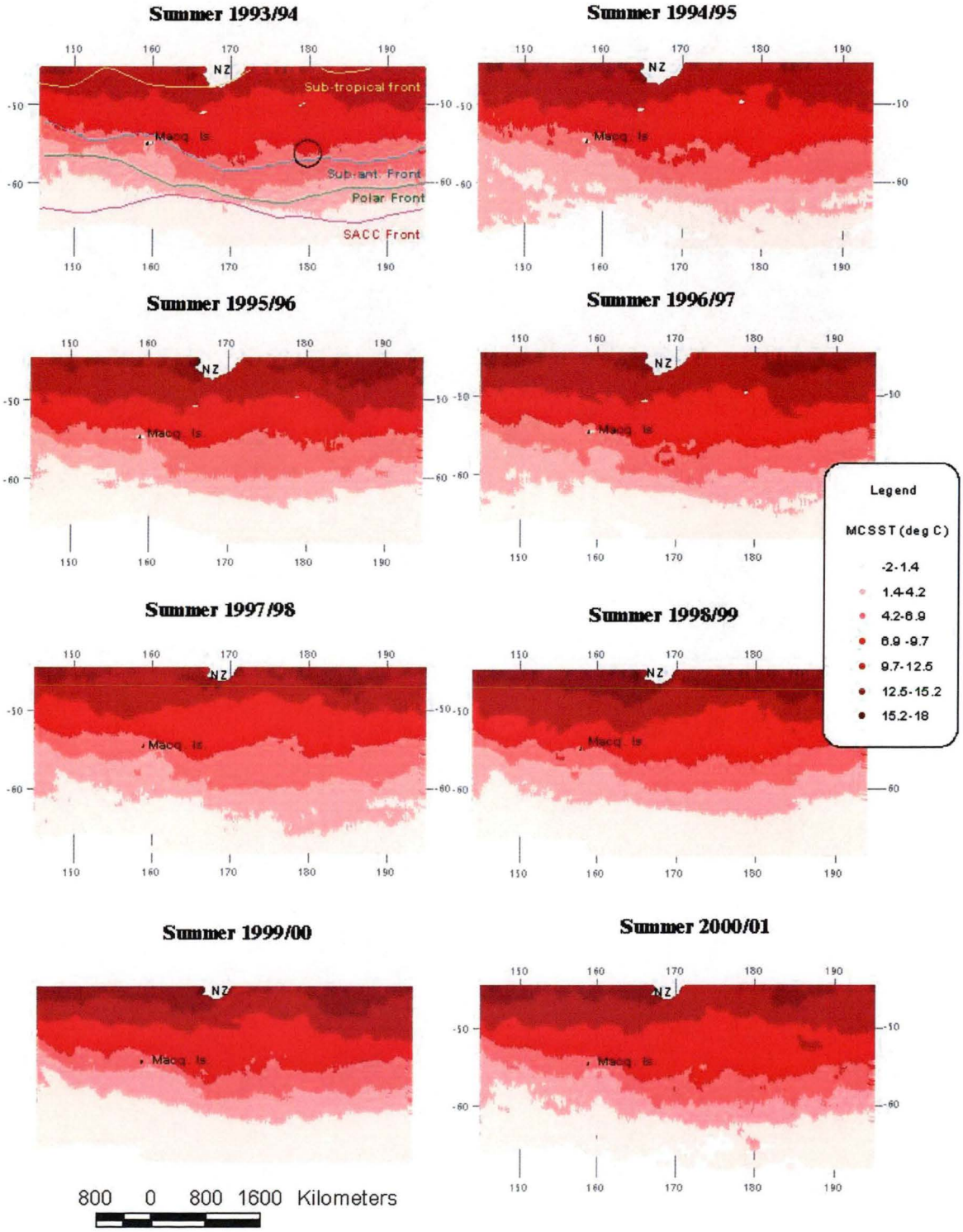


Table 4.4
Distance from Macquarie Island to colder (1.4 - 4.2°C) or warmer (6.9 - 9.7°C) temperature band

Summer	Distance to cold band (km)	Distance to warm band (km)
1993/94	0	132
1994/95	44	123
1995/96	32	102
1996/97	212	100
1997/98	113	152
1998/99	207	53
1999/00	64	155
2000/01	71	107

One of the main foraging areas of Grey-headed albatrosses from Macquarie Island can be encapsulated by a circle of 400 km diameter centred at 180°E and 56°S (see Figure 4.7, summer 1993-94 and Chapter 7). Sea surface temperatures were averaged and summed over this area for each summer season from 1993/94 to 2000/01 (Table 4.5).

Table 4.5
Mean and sum of sea surface temperatures (SST) in primary foraging region of Grey-headed albatrosses from from 1994/95 to 2000/01

Summer	Mean SST (°C)	Sum SST (°C)
1993/94	6.50	1565.4
1994/95	6.90	1360.2
1995/96	6.40	1606.6
1996/97	6.99	1965.0
1997/98	6.36	1761.8
1998/99	6.92	2014.0
1999/00	6.29	1830.3
2000/01	6.82	1692.4

Spearman rank correlations were used to test for correlations between mean and cumulative sea surface temperatures in this area and the breeding success of Grey-headed albatrosses; however, no significant correlations were found. Tests for correlations between sea surface temperatures and breeding success in the year before and the year after (to test for pre-emptive or lag effects) were also conducted with no significant results. No other detailed data on the pelagic foraging areas of the other species were available and therefore no other comparisons of this nature were made.

4.3.6.2 Chlorophyll A

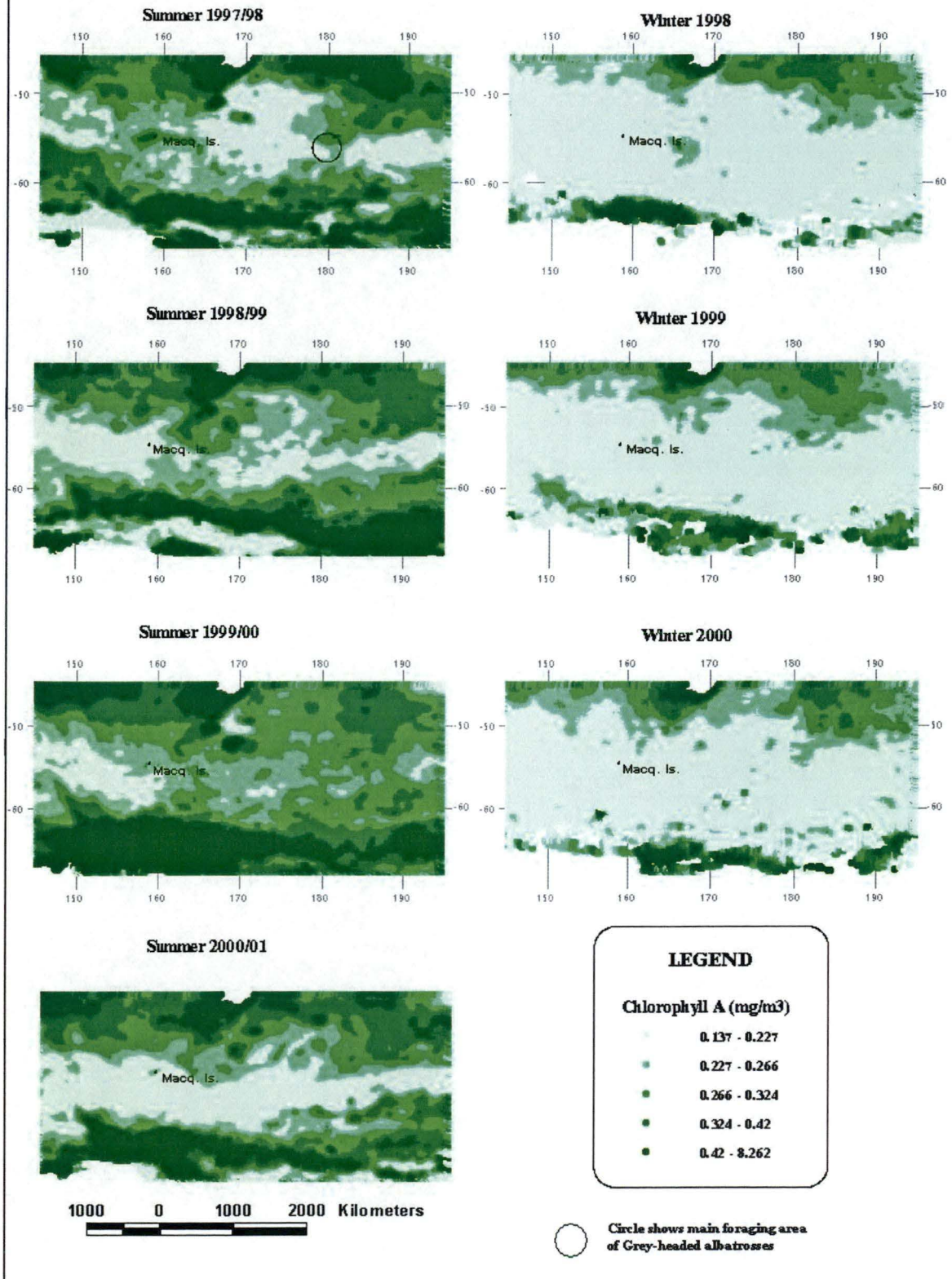
Data on chlorophyll A levels (monthly bins) were averaged from October to March inclusive (hereafter referred to as summer) and April to October inclusive (hereafter winter) using the same IDL programs and boxcar smoothing procedures as the sea-surface temperature analyses. However, unlike the sea surface temperature data, chlorophyll A data were only available from the summer of 1997/98 to the end of March 2001 (Figure 4.8). These figures (smoothed data) clearly illustrate both the inter-annual and annual variation in chlorophyll A levels in the Macquarie Island region. In an attempt to quantify this variation, mean and cumulative chlorophyll A levels were calculated in a 350 km diameter circle centred on Macquarie Island as well as the 400 km circle (foraging area of the Grey-headed albatrosses) used in the sea surface temperature analyses. Raw chlorophyll A levels were used in these qualitative analyses, as some finer scale data are lost in the smoothing procedure.

Table 4.6
Mean and sum of summer[A] and winter[B] chlorophyll A levels ($mg.m^{-3}$) around Macquarie Island and in the main foraging region of the Grey-headed albatross

Summer	350 km diameter circle around Macquarie Island		400 km circle around main foraging area of Grey-headed albatross	
	Mean	Sum	Mean	Sum
97-98 Summer	0.299	290.90	0.238	298.71
98-99 Summer	0.197	192.33	0.228	284.72
99-00 Summer	0.247	240.59	0.270	337.82
00-01 Summer	0.206	201.21	0.216	271.21
98 Winter	0.199	192.11	0.183	226.47
99 Winter	0.190	183.36	0.199	248.51
00 Winter	0.189	183.89	0.183	225.66

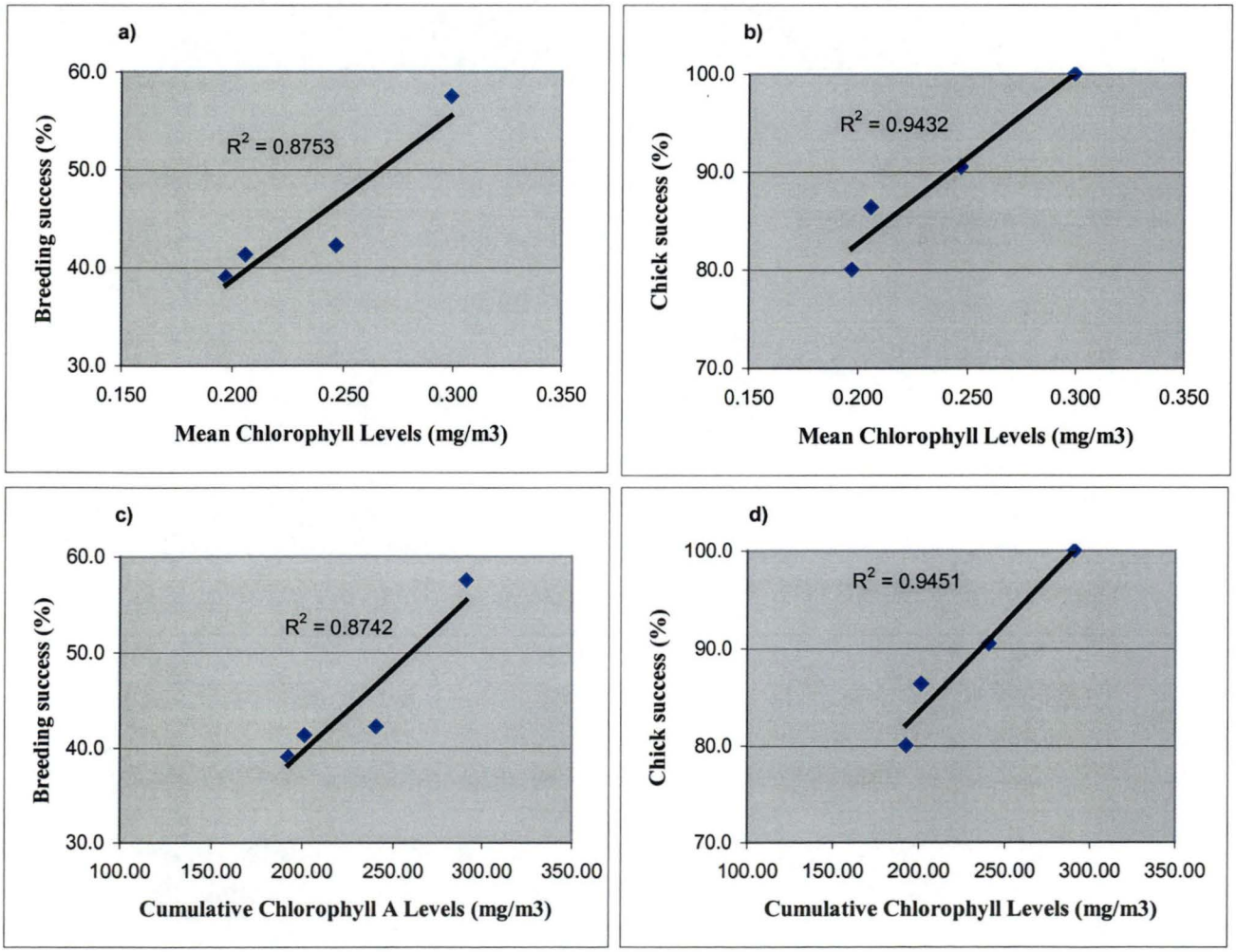
[A] October - March inclusive, [B] April - September inclusive

Figure 4.8
Variation in chlorophyll A levels during summer (October-March) and winter (April-September) around Macquarie Island from 1997/98 to 2000/01.



No correlations were found in the annual tests between overall breeding success and chlorophyll A levels around Macquarie Island. However, strong positive correlations were found between summer chlorophyll A levels and breeding success of Black-browed albatrosses in the previous year (r^s_4 = 1.0, $p<0.0001$). These values were then plotted and estimates of r^2 obtained in an attempt to quantify the strength of the linear relationship (Figures 4.9a-d). The strongest correlation was between chick success and cumulative chlorophyll A levels (r^2=0.945), but there was very little difference between cumulative chlorophyll levels and mean chlorophyll A levels (Figures 4.9b and 4.9b).

Figure 4.9
Relationship between chlorophyll A levels around Macquarie Island and Black-browed albatross breeding success in the previous year (1996/97 –2000/01)



No significant correlations were found between the breeding success of Grey-head albatrosses and chlorophyll A levels (year to year, pre-emptive and lagged) in the primary foraging area of this species.

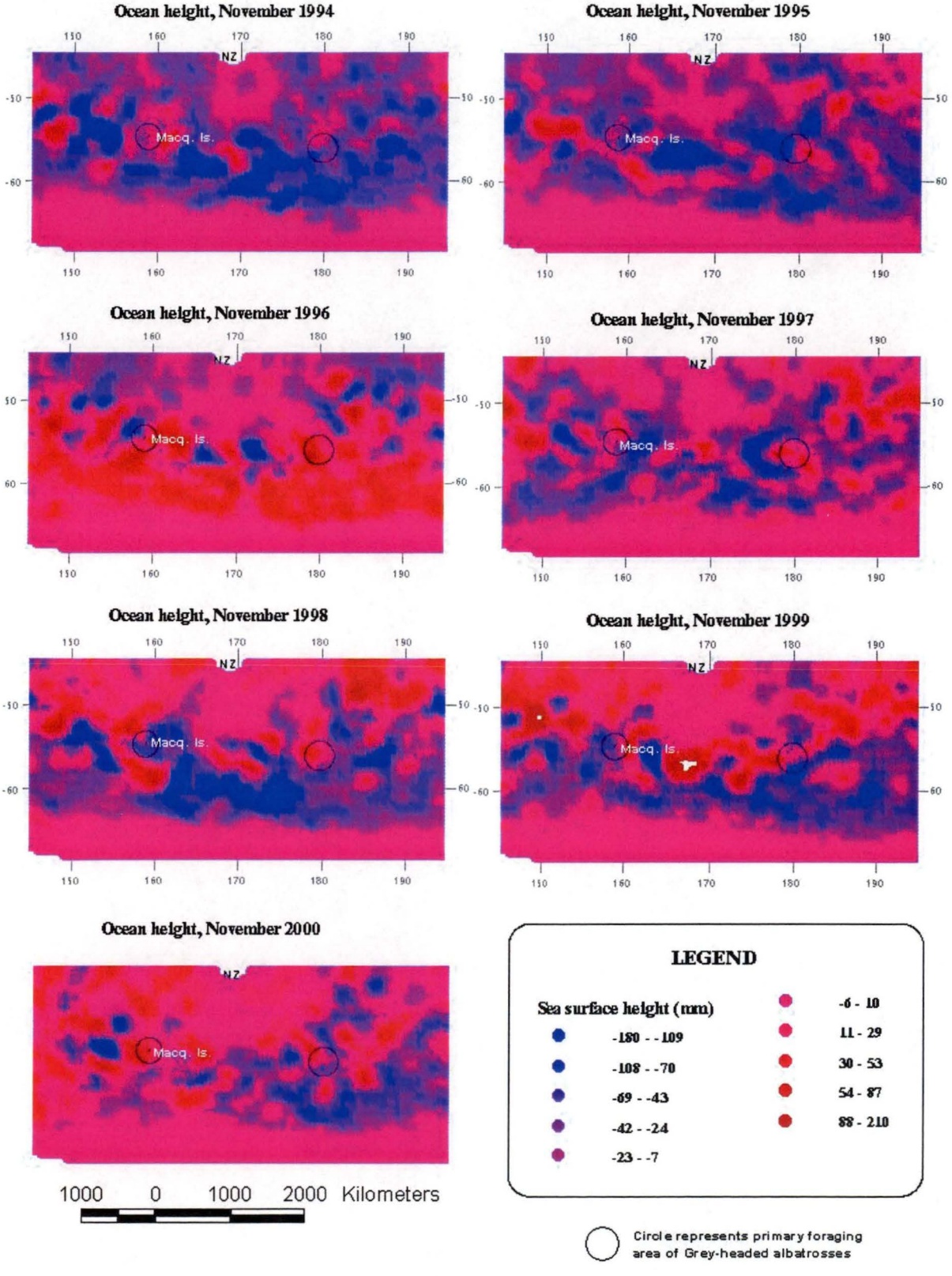
4.3.6.3 Sea surface height anomalies

In contrast to the sea surface temperature and chlorophyll A data, sea surface height anomalies data were not averaged. When successive ten-day bins of these data were examined the dynamic nature was revealed (high positive and low negative anomalies changing every ten days) and it is likely that averaging ten-day bins (even over short periods of time) would most result in the loss of most of the meaningful data. Ten-day bins were obtained from mid-November each year from 1994-2000 and smoothed using a boxcar average (kernel size=10 units). These data are shown in Figure 4.10 and clearly show that ocean height is considerably more dynamic than the sea surface temperatures or chlorophyll A levels in the Macquarie Island region. In a similar manner to the previous analyses, small areas (e.g. the Macquarie Island circle and the Grey-headed albatross foraging area circle-see Figure 4.10) were averaged and summed in order to facilitate inter-annual comparisons (Table 4.7). The absolute values of the means and sums were taken and Spearman Rank Correlation Tests conducted.

Table 4.7
Mean and sum (absolute values) of sea surface height anomalies (measured in mm) in a 350 km diameter circle around Macquarie Island and in the main foraging region of Grey-headed albatrosses (10 day average, mid-November 1994-2000)

Summer	350 km diameter circle around Macquarie Island		Main foraging area of the Grey-headed albatross	
	mean	sum	mean	sum
Nov-94	8	240	35	1369
Nov-95	20	609	58	2270
Nov-96	5	143	55	2158
Nov-97	4	131	15	581
Nov-98	32	969	19	726
Nov-99	39	1167	7	292
Nov-00	48	1446	4	141

Figure 4.10
Variation in sea surface height anomalies in a ten day period in mid-November each year from 1994 to 2000 around Macquarie Island
Positive (warm) anomalies in red, negative (cold) anomalies in blue.

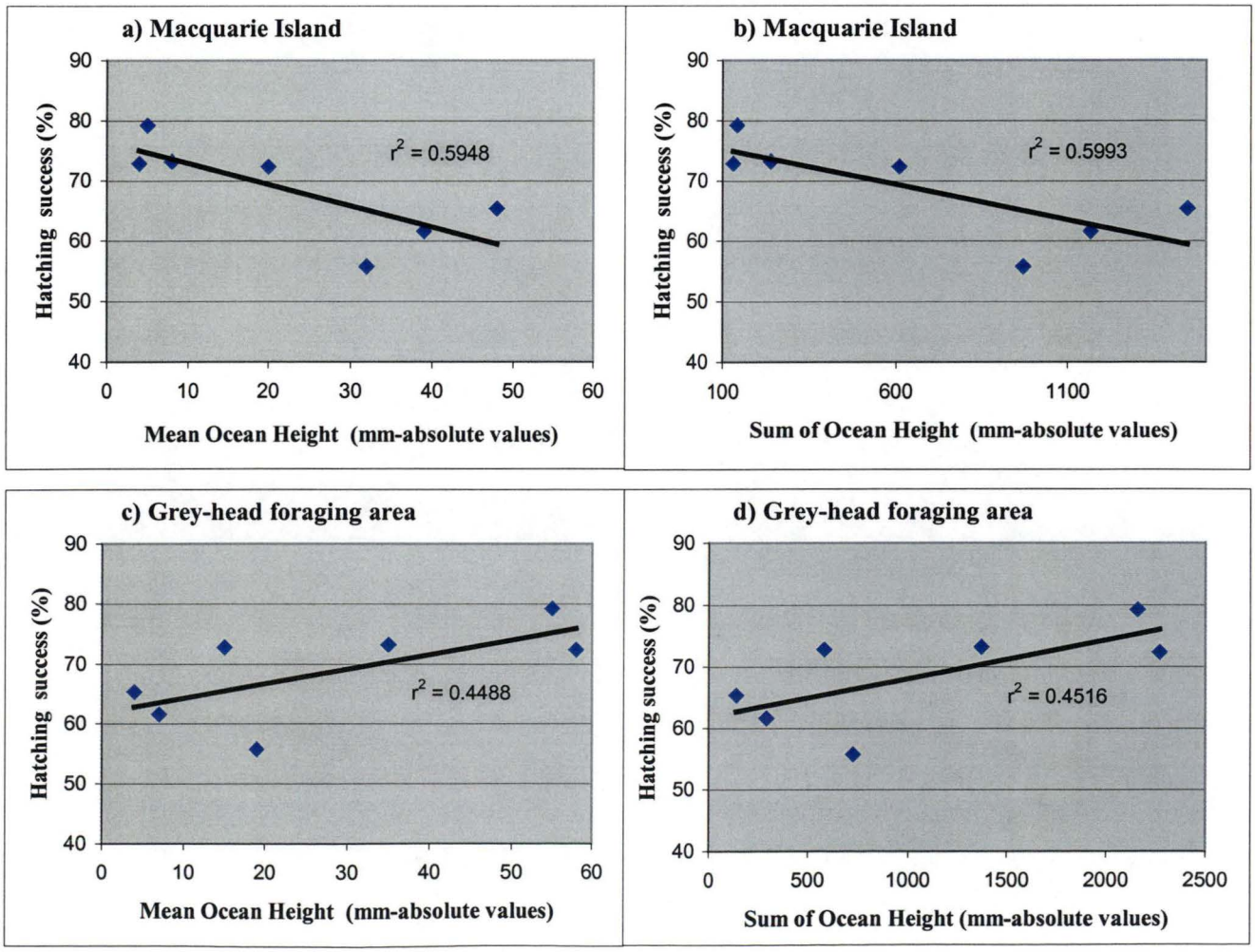


Significant negative correlations were found between absolute values of the sea surface height anomalies around Macquarie Island and the breeding success (hatching and overall) of Grey-headed albatrosses (r^s_7 = -0.75, p=0.026, r^s_7 = -0.68, p=0.047). However, the latter p-value was not significant following the False discovery correction. In addition, when these values were plotted only the correlations between hatching success and sea surface height anomalies were found to be significant (mean - r^2 = 0.595 , p = 0.021; sum - r^2 = 0.599 , p = 0.021; see Figures 4.11a-b).

No correlations were found between breeding success and mean or summed sea surface height in the Grey-headed albatross foraging circle; however, when plotted, these values yielded r^2 values indicative of a significant negative linear relationship (mean - r^2 = 0.449 , p = 0.049; sum - r^2 = 0.452 , p = 0.049; see Figures 4.11c-d). This was the only case where the Pearson Correlation Test yielded a significant result concurrently with a non-significant result from the Spearman Rank Correlation Test.

Figure 4.11

Relationship between hatching success of Grey-headed albatrosses and sea surface height anomalies at a), b) Macquarie Island and c), d) main foraging area



The result is particularly noteworthy because the nature of the correlation in the Grey-head foraging circle is positive while the correlation around Macquarie Island is negative (Figures 4.11a-d). This suggests that Grey-headed albatrosses are targeting different areas (i.e. gradients), or development stages of the anomalies when foraging in neritic or pelagic waters. Such differences may be associated with different prey items that are preferentially targeted at different stages of the breeding cycle.

4.3.7 Timing of failures and causes

4.3.7.1 Timing of failures

The date of failure for each unsuccessful breeding pair of Wandering, Black-browed and Grey-headed albatrosses was recorded as part of the daily observations of these species. These data were partitioned into 20-day intervals from the date of laying and plotted to illustrate the overall timing of failure and the respective contribution of each season (Figures 4.12, 4.13, 4.14). These figures show that the timing of failure of each species is quite different. No data on failure times of Black-browed and Grey-headed albatrosses were obtained in 1999/00 as no laying dates were recorded due to the delayed arrival of albatross project staff on Macquarie Island.

Only 30 failures of breeding Wandering albatrosses were recorded between 1994/95 and 2000/01 and the timing of failure was known for 25 of these pairs. Most failures occurred between 80 and 100 days after laying (52%), and the majority of these were non-viable eggs that were not going to hatch (no or halted embryo development). Most other failures occurred during incubation with 16% of all failures occurring in the first 20 days after laying. Only one Wandering albatross chick failed after it was two months old (140+ days after laying) and Wandering albatross chicks that reached this age almost always survived to fledging. A measure of the timing of failure each year was calculated by allocating the 20 day intervals numbers between one and nine (i.e. 1-20 = 1, 21-40=2; etc) and taking their mean (Table 4.8). This estimate allowed interspecies comparisons to be made and showed that Wandering albatrosses tend to fail later in the breeding cycle than Black-browed or Grey-headed albatrosses.

One-third of all Black-browed albatross failures occurred in the first 20 days after laying, and a further 50% of all failures occurred between day 20 and 80, with consistent rates of failure in each of these three time periods (21-40 - 18%; 41-60 – 15%; 61-80 – 17%) (Figure 4.13).

Figure 4.12
Timing of failures in Wandering albatrosses in relation to the stage of the breeding cycle (1994/95 - 2000/01)

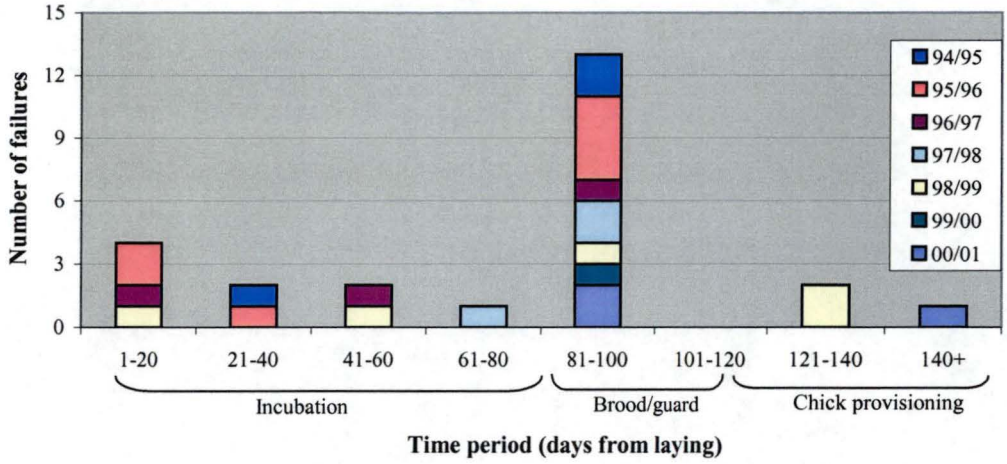


Figure 4.13
Timing of failures in Black-browed albatrosses in relation to the stage of the breeding cycle (1994/95-2000/01)

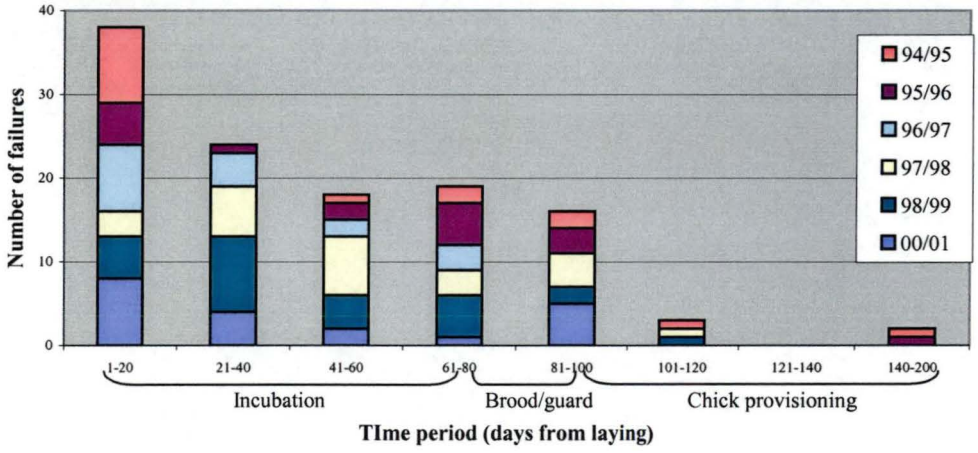
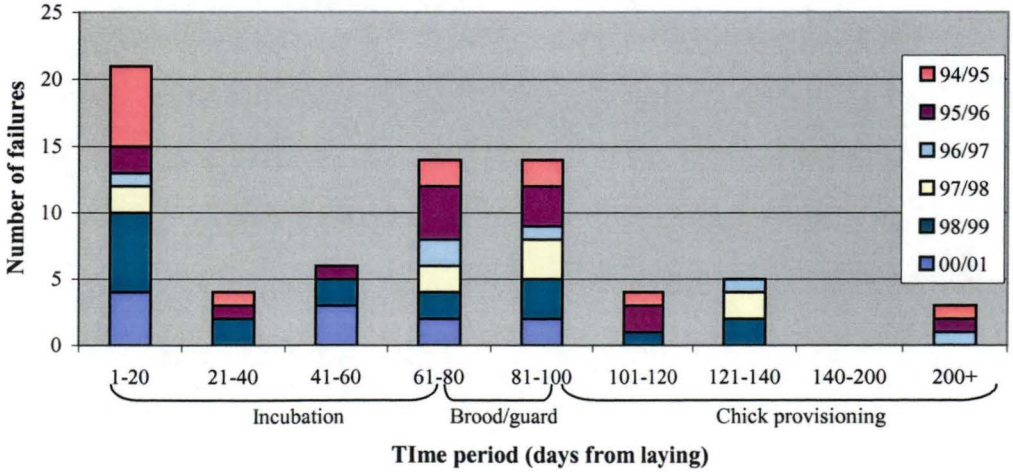


Figure 4.14
Timing of failures in Grey-headed albatrosses in relation to the stage of the breeding cycle (1994/95 - 2000/01)



The number of failures decreased after day 80 and only five percent of all failures occurred after day 100. The peak of failures occurred in the first 20 days in most seasons; however, in 1997/98 most failures occurred between 41-60 days after laying and in 1998/99 most failures occurred 21-40 days after laying. The mean annual measure of failure ranged from 2 - 3.3 and was the lowest and least variable of all the species.

Table 4.8
Mean failure time of Wandering, Black-browed, Grey-headed and Light-mantled sooty albatrosses on Macquarie Island between 1994/95 and 2000/01

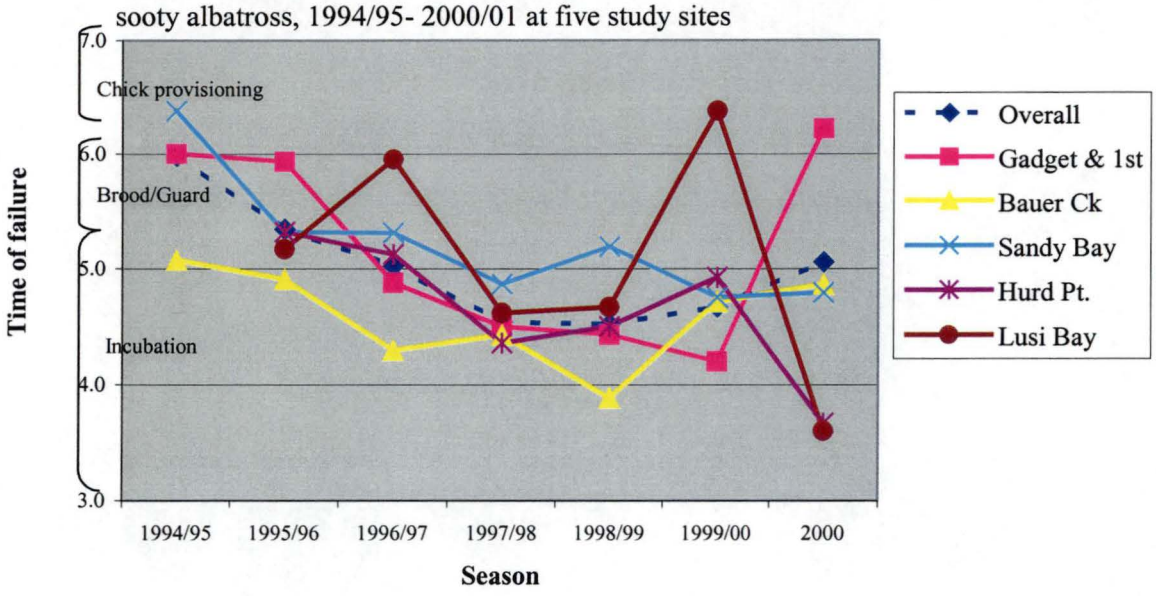
Season	Wandering Albatross	Black-browed albatross	Grey-headed albatross	Light-mantled sooty albatross
1994/95	6.0	2.6	2.8	6.0
1995/96	5.0	2.7	3.3	5.3
1996/97	4.6	3.1	4.3	5.0
1997/98	4.7	2.0	5.0	4.5
1998/99	3.0	3.3	4.2	4.5
1999/00	3.4	no data	no data	4.7
2000/01	4.0	2.8	3.2	5.1
Mean ± s.e	4.4 ± 0.4	2.8 ± 0.2	3.8 ± 0.3	5.0 ± 0.2

1= early incubation; 4-5 = hatching; 10 = fledging

The number of Grey-head failures peaked in the first 20 days of incubation then decreased through mid- incubation before increasing again during late incubation and the early brood/guard (Figure 4.14). Proportionally more Grey-headed albatross chicks failed after day 100 (17%) relative to Black-browed (5%) and Wandering albatrosses (12%). The mean annual measure of failure time was generally higher than Black-browed albatrosses but lower than Wandering albatrosses.

Due to the less frequent nest checks of the Light-mantled sooty albatrosses, the different study sites involved and the uncertainty of laying dates in most seasons, data on the timing of Light-mantled sooty albatross failures were averaged for each season and plotted with respect to the study site (Figure 4.15). The mean time of failure for each season was also calculated from pooled data from all study sites (Table 4.8, Figure 4.15).

Figure 4.15
Mean timing of failures (1=early November, 7=early February) of Light-mantled sooty albatross, 1994/95- 2000/01 at five study sites



Most failures of breeding Light-mantled sooty albatrosses occurred later in the season than the other albatross species (Table 4.8) and this trend was evident at all study sites (Figure 4.14).

There was an apparent trend in Figure 4.15 for failure dates to occur earlier from 1994/95 to 1998/99; however this is likely to be attributable to the monitoring regime beginning later in the 1994/95 and 1995/96 seasons and consequently skewing the mean failure time slightly upwards.

Although all species showed inter-annual variation in the mean failure time, only estimates for Wandering and Light-mantled sooty albatrosses were correlated (Spearman's Rank, r^s_7 = 0.80, p=0.03). These two species have the longest mean incubation shift and the ability of these species' to incubate for long periods of time may be responsible for the similarities in timing of failures. No significant correlations were found between the variation in the mean failure time and variation in breeding success of any species.

4.3.7.2 Causes of failure

In many cases, the cause of failure could not be ascertained due to the frequency of observations, particularly with the Light-mantled sooty albatross, and therefore no data on reasons for failure are presented for this species. The cause of most of the Wandering albatross failures could be identified (20 out of 30, 67%), whilst the cause of approximately

half the Black-browed albatross failures (74 out of 155) and the cause of only one-third of Grey-headed albatross failures (67 out of 225) could be ascertained. Therefore the data presented in Table 4.9 are not a truly quantitative assessment of causes of failures, and is biased towards those causes that are easiest to identify (e.g. non-viable eggs-determined by non or halted formation of the embryo, nest abandonment in some cases and nest deterioration or landslides). In addition, some of the causes are strongly inter-related (e.g. nest abandonment, poor/pair nest bond and chick starvation) and this also makes quantification of specific causes difficult.

Nevertheless, Table 4.9 gives an indication of the differences between the three species. Failures due to non-viable eggs constituted a high proportion of failures in all species, particularly in the Wandering albatrosses. This may be attributable in part to one pair of Wandering albatrosses that have failed six times since 1994/95 due to a non-viable egg and it is extremely likely that one of this pair is infertile. A high proportion of Black-browed albatrosses failed due to poor pair/nest bonds relative to the other species while Grey-headed albatrosses were the only species to have significant numbers of chicks fail close to fledgling.

Table 4.9
Causes of breeding failure of Wandering, Black-browed and Grey-headed albatrosses from 1994/95 to 2000/01 (percentages of total failures identified)

Season	**Wandering Albatross**	**Black-browed albatross**	**Grey-headed albatross**
Total failures identified	*20*	*74*	*67*
Nest abandonment	5	12	9
Damage to egg by parent	10	8	3
Poor pair/nest bond	10	18	0
Non-viable egg	60	20	22
Chick predation	10	5	3
Chick starved	0	12	6
Chick fell off nest	0	4	9
Nest deterioration/landlside	0	9	18
Human disturbance	0	5	4
Weather	5	3	6
Failed on fledging	0	3	19

Nest abandonment, poor-pair nest bond and starvation of the chick were three causes that were generally related to the non-return of one of the parents and this was most commonly observed in Black-browed albatrosses. Predation was rare, and when it occurred it was usually attributable to Skuas (*Catharacta lonnbergi*) or Giant petrels (*Macronectes giganteus, M. halli*). There was only one instance where a feral cat was implicated in the death of a Grey-headed albatross chick, and this evidence was circumstantial (1995/96 Unpublished Fieldwork Report, Environment Australia). Failures caused by human disturbance made up a small proportion of the overall failures, and all but one of the failures attributed to human disturbance occurred in the first two years of the project when many breeding birds were being banded.

The relatively high proportion of Grey-headed breeding failures that were attributed to nest deterioration/landslide is more indicative of the steep, unstable, dynamic nesting environment than the ability of this species to build a stable, long-lasting nest. The steeply sloping tussocked nesting areas may also be responsible for the relatively high number of chicks that fail close to fledging. As a chick starts to grow and exercise they become more curious and can misjudge the edge of the nest and consequently fall out, usually with fatal results as the parent will not feed a chick further than one metre or so below the nest.

4.3.7.3 Age effects on breeding success of Wandering albatrosses

The mean breeding age of the Wandering albatross breeding population in each year was documented in Chapter 3, Section 3.3.1c, Table 3.5. Spearman Rank Correlation Tests were used to test for correlations between the three measures of breeding success and the mean breeding age in each year. No correlations were found between breeding age (males and females combined) and overall success and similarly no correlations were found between breeding age and the mean time of failure each year (r^s_7 = 0.143, p=0.38). Correlations between maternal age and breeding success were also investigated and like the overall breeding age no significant correlations were found between hatching success (r_7=0.31), chick success (r_7=0.21) and overall breeding success (r_7=0.34).

4.3.8 Individual quality of breeding birds

Individual breeding records of all species were analysed from 1994/95 to 2000/01 and birds were classified as *bottom*, *medium* or *top* quality breeding birds according to the proportion of successful breeding attempts (Section 4.2.3). Table 4.10 summarises the number of breeding records analysed and the subsequent numbers of breeders in each category.

Most Wandering albatrosses that were recorded breeding could be classified as *top*, *medium* or *bottom* quality breeding birds, with only 27% not classified due to too few breeding attempts. However, approximately half of all the other species that attempted to breed could not be classified due to too few breeding attempts.

4.3.9 Individual breeder quality and trends in overall breeding success

The proportion of *top*, *medium* and *bottom* quality breeding birds in the breeding population each season was quantified for all species. A significant positive correlation was found between the proportion of *top* breeders each year and overall breeding success of Black-browed albatrosses (r^s_7 = 0.89, p=0.007). No other correlations were found between the number of *top* breeders in a breeding population and the breeding success of that year.

Table 4.10
Numbers and proportions of *top*, *medium* and *bottom* quality breeding birds (data from 1994/95 to 2000/01)

Species	Total	*Top* breeders		*Medium* breeders		*Bottom* breeders		Not classified	
		No.	%	No.	%	No.	%	No.	%
Wandering albatross [A]	44	21	47.7	7	15.9	4	9.1	12	27.3
Black-browed albatross [B]	130	25	19.2	22	16.9	19	14.6	64	49.2
Grey-headed albatross [A]	331	103	31.1	40	12.1	40	12.1	148	44.7
Light-mantled sooty albatross [A]	704	160	22.7	50	7.1	134	19.0	360	51.1

[A] Minimum of three breeding attempts for classification of biennial breeding birds

[B] Minimum of four breeding attempts for classification of annual breeding birds

4.4 DISCUSSION

4.4.1 Human impacts

It is possible that long-term monitoring programs such as the current study have negative impacts on breeding success due to the presence of researchers during the breeding season. There is no evidence that this has occurred for Wandering albatrosses and breeding success of this species showed a slightly increasing trend between 1994/95 and 2000/01. Breeding success of Black-browed albatrosses declined from 1996/97 to 1997/98; however, it was relatively stable for the three seasons preceding and the subsequent four season. There is no evidence that this decline was related to the presence of albatross project workers. There were no researchers in the area during most of the incubation period in 2000/01 and there were no differences in breeding success as a result.

The breeding success of the Grey-headed albatrosses has also varied considerably over the seven seasons, rising to a peak in the third season and decreasing in subsequent seasons before rising again this season to near average levels. Like the Black-browed albatrosses, this is not a gradually decreasing pattern that may be expected in response to the presence of investigators.

There was no statistical evidence to suggest that monitoring Light-mantled sooty nesting sites every two weeks had any significant impact on breeding success. However, the sites that were remotely monitored consistently showed a higher breeding success than those visited by researchers. Such comparisons were also confounded by environmental and topographical differences at the different sites; however, regular assessment of the impact of this long-term program is essential given the nature of these results.

4.4.2 Breeding success on Macquarie Island

4.4.2.1 Wandering albatrosses

Wandering albatrosses had the highest and most variable breeding success of the four species breeding on Macquarie Island. This variability is likely to be attributable to the small size of the breeding population and the influence that the failure of one or two pairs has on overall breeding success each year. Most Wandering albatross chicks that hatch survive to fledging, and of the 44 chicks hatched between 1994/95 and 2000/01, only four have died and overall breeding success of this species is largely driven by variation in hatching success. The high breeding success of this species relative to the other albatrosses breeding on Macquarie Island

results from many factors including: a) the pre-breeding investment into pair and nest bonding over one to three years and resultant strength of these bonds (Pickering 1989); b) its large size and stored energy reserves that make abandonment of the egg or chick unlikely (Weimerskirch 1995); c) its efficient and wide ranging foraging strategy (Prince *et al.* 1998; Weimerskirch 1998) and d) its ability to adjust its foraging strategy in relation to available resources (Weimerskirch *et al.* 1997d) or time of year (Weimerskirch and Lys 2000).

Considerably lower breeding success on Macquarie Island was reported by Carrick and Ingham (1970) between 1965 and 1968 (hatching – 61%, chick – 74% and overall – 45%). Tomkins (1985b) also documented low overall breeding success, between 1974 and 1978 (50.2 ± 10.8 s.e); however, similar to the current study chick success was considerably higher than hatching success (72.6 ± 18.7 c.f 59 ± 10.5). The historically lower overall breeding success appears to be related to a decrease of both hatching success and chick success. In the absence of concurrent detailed demographic data it is difficult to identify the possible mechanisms behind these differences. The survivorship of adult birds was lower prior in the 1960's and 1970's (Chapter 3) and the non-return of a parent would result in nest failure and contribute to a lower breeding success. In addition, the highly invasive levels of recreational and research mediated disturbance of nesting birds prior to the late 1980's could also have contributed to decreased breeding success; and breeding success in the southern breeding grounds was significantly higher after the closure was initiated in 1986 (mean 1963-1986-62%, mean 1987-2001-72%, $t_{35} = -1.95$, p=0.03). Such information validates the introduction of the closure and emphasises the potential impact that human disturbance can have on this species.

4.4.2.2 Black-browed albatrosses

Overall breeding success of Black-browed albatrosses on Macquarie Island was the lowest of all the albatross species between 1994/95 and 2000/01. Both hatching success and chick success contributed to the variation in overall breeding success; although the contribution of each varied between years. Hatching success was more closely correlated with overall success between 1994/95 and 1998/99; however, since 1999/00, chick success emerged as the major factor in determining overall breeding success.

Breeding success of Black-browed albatross on Macquarie Island between 1977/78 and 1984/85 was described by Copson (1988). His mean estimate of overall success (66 ± 17.4 s.d) was significantly higher than the mean breeding success found between 1994/95 and 2000/01 (46.1 ± 3.6 s.e, $\chi^2_1=5.6$, p=0.018); however as discussed in Chapter 3, these

differences are likely to be attributable to an underestimate of breeding numbers in the early study. Further evidence for this hypothesis was found when hatching success and chick success from the two studies were compared. The hatching success reported by Copson (1988) was significantly higher than that found in the current study (χ^2_1=5.6, p=0.018); however chick success was not (χ^2_1=2.6, p=0.109). This is consistent with an underestimate of breeding numbers.

The proclivity of Black-browed albatrosses to fail early in the breeding season may be an indication of inferior pair and nest bonds that are formed more quickly than other albatross species (Croxall 1998). Black-browed albatrosses change partners more frequently than the other albatrosses on Macquarie Island (Chapter 5) and this also may be indicative of weaker pair bonds.

4.4.2.3 Grey-headed albatrosses

Mean breeding success of this species since 1994/95 was similar, although less variable, than that of the Wandering albatross. However, in contrast to the Wandering albatross, this variation was more equitably determined by both hatching success and chick success. The only other reports of breeding success of this species on Macquarie Island was provided by Copson (1988), and similarly to Black-browed albatrosses, estimates of breeding success from this earlier study were significantly higher (χ^2_1=5.3, p=0.021). This was attributable to significantly higher hatching success (χ^2_1=3.9, p=0.048) and there was no evidence that chick success was different to that documented between 1994/95 and 2000/01 (χ^2_1=1.5, p=0.225).

4.4.2.4 Light-mantled sooty albatrosses

Mean breeding success of Light-mantled sooty albatrosses was similar to that of Black-browed albatrosses, however, little inter-annual variation occurred between 1994/95 and 2000/01. Underlying this temporal consistency was significant spatial variation with significantly different breeding success between study sites in the north and south of Macquarie Island.

Mean breeding success of this species at three sites in the north of the island (Gadget and First, North Head and Bauer Creek) between 19970/71 and 1980/81 was 51% (Kerry and Garland 1984). This was very similar to the pooled values for the whole island found in the current study (51 ± 2%). However, when breeding success is calculated for Gadget and First Gullies, North Head and Bauer Creek only from 1994/95 – 2000/01, mean breeding success

was 33 ± 5%, providing some evidence that breeding success has declined at these sites from the 1970's to the 1990's.

There were significant and consistent differences in the breeding success of the study sites in the north Macquarie Island compared with those in the south. The higher breeding success at the southern sites appears anomalous and is likely to be due to a combination of several factors. It is possible that the different topography and environments covered by the northern and southern study sites influence breeding success. Environment and topography affect factors such as prevailing wind, location of nests and vulnerability to predators and ticks, all of, which may have some impact on breeding success. Birds breeding at the different sites may forage in different areas and this may also impact on breeding success. This could also be linked to changes in attendance patterns and subsequently nest desertion, which appears to occur more frequently in the sites of generally lower success. Attendance studies at both northern and southern sites and investigation of the foraging ecology of breeders at different sites would be useful in determining factors that could account for these inter-site differences.

4.4.3 Comparisons with other locations

The overall breeding success of these four species has been reported at other locations and available data are summarised below in Table 4.11.

4.4.3.1 Wandering albatrosses

Wandering albatrosses from Macquarie Island had the lowest overall breeding success of four subantarctic locations compared; however, due to relatively high inter-annual variation, there were no significant differences between the four sites (*D. gibsoni* excluded-no annual data) (χ^2_3=2.02, p=0.5). The breeding success of this species has increased over the last two decades at Iles Crozet (Weimerskirch *et al.* 1998) and Bird Island, South Georgia (Croxall *et al.* 1998) and there is some indication of an increase in the breeding success at Macquarie Island. However, the sample size used in the Macquarie Island study is significantly smaller resulting in more inter-annual variation and consequently trends in breeding success are more difficult to conclusively identify.

A number of studies have suggested that breeding success of this species is age related (e.g. Lequette and Weimerskirch 1990; Croxall *et al.* 1992; Weimerskirch 1992a); however, no obvious age effects were found in the current study.

Table 4.1
Breeding success of Wandering, Black-browed, Grey-headed and Light-mantled sooty albatrosses and similar conspecifics at five sub-antarctic locations

	Hatching Success		Chick Success		Breeding success		
Location	**Time period**	**% ± s.e**	**Time period**	**% ± s.e**	**Time period**	**% ± s.e**	**Source**
Wandering albatross (*Diomedea exulans*)							
Macquarie Island	1995-2001	64 ± 7	1995-2001	93 ± 3	1995-2001	60 ± 7	This study
South Georgia	1976-1990	73 ± 1	1976-1990	87 ± 2	1976-1990	64 ± 2	Croxall et al (1990)
Iles Crozet	1982-1990	84 ± 1[A]	1982-1990	91 ± 0.5[A]	1966-1995	69 ± 11[B]	[A] Weimerskirch (1992) [B] Weimerskirch and Jouventin (1998)
Gibson's albatross (*Diomedea gibsoni*)							
Auckland Islands	-	-	-	-	1991-1997	67 ± 3	Walker and Elliot (1999)
Antipodean albatross (*Diomedea antipodensis*)							
Antipodes Islands	-	-	-	-	1994-1997	76	Graeme Elliot and Kath Walker unpublished data in Walker and Elliot (1999)
Amsterdam albatross (*Diomedea amsterdamensis*)					1983-1994	71.6	Weimerskirch et al. 1997a
Amsterdam Island	-	-	-	-			
Black-browed albatross (*Thalassarche melanophrys*)							
Macquarie Island	1995-2001	54 ± 3	1995-2001	85 ± 4	1995-2001	46 ± 4	This study
South Georgia	1976-1996	62 ± 5	1976-1996	43 ± 8	1976-1996	27 ± 5	Croxall *et al*. (1998)
Iles Kergualen	-	-	-	-	1979-1995	63 ± 10	Weimerskirch and Jouventin (1998)
Campbell albatross (*Thalassarche impavida*)							
Campbell Island	1984-1996	86 ± 2	1984-1996	79 ± 5	1984-1996	66 ± 5	Waugh *et al.* (1999)
Grey headed albatross (*Thalassarch chyrsostoma*)							
Macquarie Island	1995-2001	69 ± 3	1995-2001	80 ± 3	1995-2001	55 ± 4	This study
South Georgia	1976-1996	60 ± 5	1976-1996	65 ± 4	1976-1996	39 ± 5	Croxall *et al.* (1998)
Campbell Island	1984-1996	80 ± 4	1984-1996	51 ± 11	1984-1996	40 ± 9	Waugh *et al.* (1999)
Light-mantled sooty albatross (*Pheobatria palpebrata*)							
Macquarie Island	-	-	-	-	1995-2001	51 ± 2	This study
South Georgia	-	-	-	-	1976/77	47	Thomas *et al.* (1983)
Iles Crozet	-	-	-	-	1974/75	31	Berruti (1979)
Marion Island	-	-	-	-	1968/69	50	Mougin (1970) cited in Berruti (1979)

Although chick success was higher than hatching success at Macquarie Island, South Georgia and Iles Crozet, there were marked differences in the contribution of hatching and chick success to overall breeding success on Macquarie Island compared to South Georgia. Using similar methodology to that used in the current study (e.g. Brown 1988), Croxall *et al.* (1998) found that hatching success and chick success both contributed equally to the variation in overall success; however, similarly to the current study, these authors found no correlation between chick success and hatching success. Hatching success accounted for almost 90% of the variation in overall breeding success on Macquarie Island and this is largely attributable to the consistently high chick success observed every year.

The contribution of hatching success and chick success to variation in overall breeding success on Macquarie island was more similar to that observed on Isles Crozet (Weimerskirch 1992a) and overall chick success is also more similar at the two study sites (Table 4.11). This may be attributable to available food resources and foraging ecology during the chick rearing stage. These two populations were found to be most similar in terms of population trends in Chapter 3 and it is possible that similar factors are also responsible for similar trends and magnitudes of breeding success. This species is known to forage over a wide oceanic range (Jouventin and Weimerskirch 1990) during both incubation (Weimerskirch *et al.* 1994b; Weimerskirch *et al.* 1997d) and chick rearing (Arnould *et al.* 1996; Weimerskirch *et al.* 1997b). Therefore it is possible that both populations are utilising similar Indian Ocean resources, and respond in similar ways to fluctuations in these resources.

4.4.3.2 Black-browed albatrosses

Mean overall breeding success of Black-browed albatrosses was higher than that observed on Bird Island, South Georgia and lower than that observed on Iles Kerguelen and Campbell Island (*T. impavida*) (Croxall *et al.* 1998; Weimerskirch *et al.* 1998; Waugh *et al.* 1999b). Many studies have attributed inter-annual variation in breeding success of this species to fluctuations in marine resources, particularly krill (e.g. Prince *et al.* 1994; Veit and Prince 1997). However, in a review of the food of albatrosses, Cherel and Klages (1998) showed how diets of the same species often differ in relation to breeding location. Further, there is substantial evidence that Black-brows breeding in the Indian Ocean are less dependent on krill than their Atlantic Ocean counterparts (Weimerskirch *et al.* 1986; Cherel *et al.* 2000). Prince *et al.* (1994) suggested that this inter-dependence from krill of Black-browed albatrosses breeding in the Indian Ocean was responsible for the higher breeding success observed at those locations. Differences in diet and therefore foraging regime may also be responsible for the differences in mean breeding success between Macquarie Island and the

other comparable subantarctic locations. However, with few data on the diet of this species on Macquarie Island this remains speculation.

In contrast to populations at Bird Island (*T. melanophrys*) and Campbell Island (*T. impavida*), Black-browed albatrosses from Macquarie Island had significantly higher chick success than hatching success. However, the magnitude of chick success was very similar at Macquarie and Campbell Islands and this may be due to similarities in foraging strategies and/or resources during this stage of the breeding cycle (see Chapter 8, Waugh *et al.* 1999a; Waugh *et al.* 2000). Similar to Macquarie Island, chick success of the Campbell albatross was also highly correlated with overall success on Campbell Island ($r^s_8 = 0.94$, p=0.002). However, the contribution of hatching success and chick success to variation in overall breeding success was different to that observed on Bird Island where 85% of the variation was explained by chick success (Croxall *et al.* 1998), compared to just 32% on Macquarie Island. The interactions between hatching success, chick success and overall breeding success of this species are complex (Prince *et al.* 1994) and are also likely to be influenced by the different time periods spanned by the studies being compared as well as the different sample sizes.

Breeding success of Black-browed albatrosses on Macquarie Island also appeared to be lower in years when trawling operations were being conducted earlier in the breeding season throughout the incubation period. Such a decrease could be related to a) breeding birds being distracted by the vessel and undertaking longer than 'normal' foraging trips leading to higher rates of nest abandonment or b) success could have been artificially inflated by provisioning due to offal and other discards from the vessel. Short term benefits from utilising of offal and fisheries discards has been documented for some Black-browed albatross populations (e.g. Thompson and Riddy 1995); however, it is a requirement of the fishing permit that no discards be released from this vessel in the Macquarie Island EEZ (except in an emergency) and therefore the former relationship between the presence of the fishery and breeding success seems more likely. No association between breeding success and fisheries were identified by the studies on the Campbell and Black-browed albatrosses breeding on Campbell Island or South Georgia (Waugh *et al.* 1999b; Croxall *et al.* 1998).

Nevertheless it seems clear that patterns and trends of breeding success of Black-browed albatrosses at Macquarie Island are most similar to its conspecific at Campbell Island, and least similar to that observed on Bird Island. The proximity of Macquarie Island and Campbell Island is likely to be a factor in these similarities and it is possible that oceanic resources utilised by this two closely related species at the two sites underwent similar and concurrent fluctuations.

4.4.3.3 Grey-headed albatrosses

Comparable data on the breeding success of this species were only available for Bird Island and Campbell Island. The Macquarie Island population showed the highest mean breeding success of these three locations and again, this could be largely attributed to a significantly higher chick success. Like the Black-browed albatrosses, different time periods spanned by the three studies make meaningful comparisons difficult and significant differences in the sample sizes may also confound meaningful comparisons to a certain extent. Considerable variation was observed in breeding success at both Bird Island and Campbell Island although in both cases no trend was evident (Prince *et al.* 1994; Waugh *et al.* 1999b). Both studies suggested that the mainly pelagic foraging strategy of this species made it dependent on fluctuations in marine resources, particularly fish and squid. Other studies have also shown that Grey-headed albatrosses target areas of ocean where there are likely to be concentrations of this type of marine resource (Waugh *et al.* 2000, Nel *et al.* 2000; Nel *et al.* 2001). Individual Grey-headed albatrosses from Macquarie Island consistently targeted similar areas on pelagic foraging trips and it seems likely such adherence to the 'central place foraging strategy' makes them vulnerable to fluctuations in these areas. Overall breeding success was correlated with both hatching success and chick success on Macquarie Island and this was also observed at Campbell Island.

4.4.3.4 Light-mantled sooty albatrosses

There are few comparable data on the breeding success of Light-mantled sooty albatrosses from other locations with all estimates from significantly smaller sample sizes in a single breeding season (Thomas *et al.* 1983; Berruti 1979). The Macquarie island estimates are similar or higher than these estimates; however singular nature of the estimates from other locations in addition to the differences in sample size makes comparisons almost meaningless.

4.4.4 Factors influencing breeding success

The factors responsible for the variation observed in breeding success over time on Macquarie Island and the differences between the different locations are complex and foraging ecology, particularly the fluctuation in available prey, is likely to be a major factor. Other factors that influence breeding success include disruption of attendance patterns and nest abandonment, inexperience of first time breeders, changes in partner fidelity, chick provisioning regimes and fisheries in the area, and individual breeding quality. The quality of individual breeders was an important factor, particularly with the Black-browed albatrosses. However, in contrast

to Cobley (1998) no such association was found with overall breeding success of the Grey-headed albatrosses and the proportion of *top* breeding birds in that year.

4.4.4.1 Oceanic Productivity

The availability of oceanic food resources and the patchy nature of its distribution have played an important role in the evolution of many of the life history aspects characteristic of long-lived seabirds such as albatrosses (Lack 1968; Ashmole 1971). Many studies have linked the availability of food to the variation in breeding success of most albatross species; however, the abundance of most prey items on which albatrosses feed are difficult to quantify (Hunt and Schneider 1988). Remote sensing of oceanographic features such as sea-surface temperatures, chlorophyll A levels and data on sea surface height anomalies have provided broad scale oceanographic data that can be analysed concurrently with data on predator foraging movements and life history parameters. Changes in these oceanographic data were analysed concurrently with changes in breeding success of the four albatross species breeding on Macquarie Island. These analyses represent a preliminary attempt to examine the relationship between breeding success and surrounding oceanography.

4.4.4.1a Sea Surface Temperature

Several studies have documented changes in seabird abundance in response to changing sea-surface temperatures (e.g. Hunt *et al.* 1992; Veit *et al.* 1997; Oedekoven *et al.* 2001). Other studies have linked changes in life history aspects such as breeding performance and body condition of Blue petrels (*Halobaena caerulea*) breeding on Iles Kerguelen to warm sea-surface temperature anomalies (Guinet *et al.* 1998) and ocean climate has been implicated in changing population dynamics of Atlantic fulmars (*Fulmarus glacialis*) (Thompson and Ollason 2001). The only species whose breeding success appeared to be linked to changes in sea surface temperature around Macquarie Island were the Light-mantled sooty albatrosses. The breeding success of this species was higher in years where colder waters were closer to Macquarie Island. This was a coarse method of analysing the effect of sea-surface temperatures, but the patchy nature of the satellite data did not allow accurate means to be calculated on the small geographic scale required for more detailed analyses.

Light-mantled sooty albatrosses are known to have one of the most southerly foraging ranges of the albatrosses breeding on Macquarie Island (Thomas 1982; Weimerskirch *et al.* 1986; Weimerskirch and Robertson 1994) suggesting that this species preferentially feeds on prey items inhabiting colder waters. This species also shows alternative long and short foraging patterns during chick rearing (Chapter 8) and forages in near-shore waters for significant

periods. It is possible that as colder waters move closer to Macquarie Island, prey items that Light-mantled sooty albatrosses preferentially feed on are found in higher abundance and this may facilitate an increase in breeding success.

4.4.4.1b Primary productivity

Significant positive correlations were found between chick success of Black-browed albatrosses and chlorophyll A levels in the following summer. The mechanisms that link primary production to the prey items of albatrosses are extremely complex and one of the biggest challenges facing food chain modellers today (e.g. Cherel and Weimerskirch 1995; Reid *et al.* 2001). It seems likely that oceanographic conditions that precede high levels of chlorophyll A around Macquarie Island are conducive for the prey items on which this species forages. The specifics of this mechanism are beyond the scope of the current study but it is possible that it is related to the documented affinity of Black-browed albatrosses for krill or micronekton (Croxall *et al.* 1997; Nevitt 1999).

4.4.4.1c Sea surface height anomaly

Sea surface height anomalies are identified by differences in height between neighbouring water masses and are usually indicative of currents or eddies (Park and Gamberoni 1995). Such hydrographic features have been linked to the distribution of seabirds and are likely to influence the distribution of prey (Abrams 1985; Abrams and Lutjeharms 1986; Ansorge *et al.* 1999). Sea surface height anomalies were quantified (averaged and summed) in a 350 km diameter circle around Macquarie Island and in a 400 km circle encapsulating one of the main foraging areas of the Grey-headed albatrosses. The absolute values of these data were then taken as for the purposes of the analyses it did not matter if there were positive or negative anomalies. The only species from Macquarie Island to show any correlation with these data were Grey-headed albatrosses; however conflicting trends were observed in pelagic waters (positive trend) relative to waters around Macquarie Island (negative trend).

Recent studies have shown that Grey-headed albatrosses from Marion Island target large-scale oceanographic features (specifically eddies) identified by these sea surface height anomalies (Nel *et al.* 2001). These authors showed that this species foraged preferentially at the edges of these anomalies, and that positive sea surface height anomaly data were indicative of warm anticyclonic eddies and negative values reflected colder cyclonic eddies. Warm and cold eddies were observed in the region around Macquarie Island and it appeared that Grey-headed albatrosses were targeting these eddies in a similar way to the Grey-headed albatrosses from Marion Island. Further evidence of Grey-headed albatrosses from Macquarie

Island foraging preferentially at the edges of the sea surface height anomalies is provided by satellite telemetry data in Chapter 7. If we assume that breeding success is correlated with prey abundance and that the presence or absence of these prey is inextricably linked to these anomalies, then the contrasting correlations found here may reflect the different prey items targeted by this species in near-shore as opposed to pelagic waters. These results are consistent with those presented by Nel *et al.* (2001) and are potentially indicative of different foraging strategies in pelagic and neritic waters.

The three small breeding populations of albatrosses on Macquarie Island are particularly vulnerable to changes in life history parameters such as breeding success that influence their long-term survival. The preliminary analyses presented here suggest that changes in oceanic resources are linked to the breeding success of the albatrosses on Macquarie Island, and consequently changes in oceanic resource availability are likely to play a role in future population trends. Continued monitoring of foraging ecology and oceanic resources are required to allow changes in these parameters to be identified before impacts are observed on population numbers.

Chapter 5 - The breeding frequency of albatrosses on Macquarie Island

5.1 INTRODUCTION

Procellariiformes typically exhibit a very low fecundity with only one egg laid at each breeding attempt and no potential for a replacement egg (Warham 1990). Lack (1968) contended that breeding parameters such as clutch size and frequency of breeding evolved to maximise the number of surviving young and suggested that this was inextricably linked to foraging ecology and available food supply. However, Ricklefs (1990) questioned this connection between available food and life history attributes and suggested that many aspects of seabird breeding biology and provisioning facilitated the survival of the young in times of variable food supply. Whatever the evolutionary strategy, it is clear that breeding frequency of Procellariiformes (specifically albatrosses) is dependent on the interplay of a complex suite of ecological, behavioural and physiological factors (Drent and Daan 1980; Jouventin and Weimerskirch 1988; Croxall 1991; Boggs 1992).

The complexity of the interrelationships between factors that influence breeding frequency makes it difficult to quantify the impact of single factors. Underlying the deferral of breeding exhibited by many species is the extended chick rearing period on a low energy diet and the reduced time available for the female to regain breeding condition (Croxall 1991). However, several studies have documented the influence of specific factors on the reproductive 'decision making' process. Drent and Daan (1980) reported that body condition was likely to influence the reproductive decision in many species of terrestrial birds and other studies have shown this to be the case in both smaller (Chastel *et al.* 1995) and larger Procellariiformes (Croxall 1991; Weimerskirch 1992a).

Age and breeding experience were identified as influential factors in the breeding frequency of Antarctic fulmars (Weimerskirch 1990), Wandering albatrosses (Croxall *et al.* 1990; Croxall *et al.* 1992; Weimerskirch 1992a) and Grey-headed albatrosses (Cobley *et al.* 1998). Studies have also shown that physiological factors such as endocrine processes (Hector *et al.* 1985; Hector *et al.* 1986) and moult regimes (Langston and Rohwer 1996; Cobley and Prince 1998) also play a role in determining breeding frequency. Other documented influential factors include: body size (Barbraud *et al.* 1999), foraging ecology (Prince 1985; Jouventin and Weimerskirch 1988), changes in breeding site availability (Chastel *et al.* 1993) and loss or change of mate (Ollason and Dunnett 1988).

Breeding success is often inextricably linked to breeding frequency, particularly in biennially breeding species, as the timing of failure defines the time available to prepare for the next breeding attempt (Chastel 1995). Wandering albatrosses, with a typical nestling period of around 350-360 days is one of the few species that appears physiologically unable to breed in successive years if successful (Hector *et al.* 1985). Most Wandering albatrosses breed biennially if successful but deferral of breeding for three or more years has also been documented (Jouventin and Weimerskirch 1988; Croxall *et al.* 1990; Croxall 1991). Grey-headed albatrosses and Light-mantled sooty albatrosses also typically have at least one season off after a successful breeding attempt (Tickell and Pinder 1967; Jouventin and Weimerskirch 1988; Croxall 1991); however, in contrast to Wandering albatrosses, rare cases of successive successful breeding attempts have also been documented and in most cases the returning birds were males. Breeding success has less impact on the breeding frequency of Black-browed albatrosses as this species generally breeds in successive years regardless of the outcome of the prior breeding attempt (Tickell and Pinder 1967; Jouventin and Weimerskirch 1988.

The investigation of breeding frequency is integral to any study of population dynamics. Changes in breeding frequency often occur concurrently with changes in survivorship or breeding numbers (Jouventin and Weimerskirch 1988) and can also illustrate different foraging strategies or regimes (Prince *et al.* 1994). The breeding frequency patterns of the four albatross species breeding on Macquarie Island are presented here and the extent to which each species adheres to a biennial or annual breeding pattern is quantified. Comparisons are made with breeding frequency patterns of these species at other subantarctic locations and the influence of this parameter in relation to other aspects of life-history is also discussed.

5.1.2 Summary of research questions

1. What is the breeding frequency pattern of each of the four albatross species on Macquarie Island ?

2. Does breeding frequency vary in relation to the quality of individual breeding birds ?

3. Are these breeding frequency patterns similar to those observed at other subantarctic locations ?

4. What are the implications of the different breeding frequency strategies for life history attributes and long-term viability of these species on Macquarie Island ?

5.2 DATA PROCESSING AND ANALYSES

5.2.1 Breeding Frequency

The breeding records of individuals were derived from the resight datasets used in Chapter 3 (Section 3.2) prior to the partitioning of these datasets into chick and adult subsets. Only data obtained in the current study (i.e. 1994/95-2000/01) were used. Data on the success or failure of each breeding attempt, any partner changes (all species) or location changes (Black-browed albatrosses only) were collated. These data were then summarised in breeding frequency tables showing the proportion of birds returning *n* years after a successful or unsuccessful breeding attempt.

Data from the entire breeding populations of Wandering, Black-browed and Grey-headed albatrosses, and from a sub-sample (five study sites) of the Light-mantled sooty albatross breeding population, were utilised in the analyses. The Light-mantled sooty albatross study sites used were Sandy Bay, Gadgets and First Gully, Bauer Creek, slopes north of Hurd Point and Lusitania Bay, and were chosen on the basis of long-term data and accessible nests. Sites with many inaccessible nests each year (e.g. North Head) were excluded as a high proportion of unidentified birds were present each year.

Overall breeding frequencies were calculated by dividing the total number of returning birds in each category (n+1, n+2 etc) by the total number of identified birds in the corresponding years. Therefore these 'overall' values were independent of each other and could not be summed to calculate overall return rates.

5.2.2 Individual breeder quality

The breeding quality of individual breeding birds as defined in Chapter 4 (see 4.2.2 for details) was used to examine differences in breeding frequency of *top*, *medium* and *bottom* quality breeding birds from each species

5.3 RESULTS

5.3.1 Wandering albatrosses

Wandering albatrosses are consistent biennial breeders with 90% (n=62) of successful breeders returning to breed after missing a year. The data are summarised below in Table 5.1.

Table 5.1
Breeding frequency of Wandering albatrosses in relation to breeding success (1994/95 - 2000/01)

		% breeding for next time in subsequent season						
Season	**Number of identified birds**	**1**	**2**	**3**	**4**	**5**	**6**	**Total**
Successful breeders								
1994/95	12	0.0	100.0	0.0	0.0	0.0	0.0	100.0
1995/96	6	0.0	66.7	16.7	0.0	0.0		83.4
1996/97	16	0.0	100.0	0.0	0.0			100.0
1997/98	8	0.0	100.0	0.0				100.0
1998/99	20	0.0	80.0					80.0
1999/00	12	0.0						0.0
Total	74	*0.0*	*90.3*	*2.4*	*0.0*	*0.0*	*0.0*	
Unsuccessful breeders								
1994/95	8	87.5	0.0	0.0	0.0	0.0	0.0	87.5
1995/96	11	72.7	0.0	0.0	9.1	18.2		100.0
1996/97	6	100.0	0.0	0.0	0.0			100.0
1997/98	10	100.0	0.0	0.0				100.0
1998/99	10	80.0	20.0					100.0
1999/00	2	100.0						100.0
Total	45	*83.7*	*4.3*	*2.7*	*4.0*	*9.5*	*0.0*	

As the population is small, changes in return rates of one or two birds can significantly influence these percentages. Only one successful breeder returned to breed after missing two seasons. Eighty-four percent of unsuccessful breeders returned to breed the following year. Most deferral of breeding by successful breeders could be attributed to the non-return of a partner. The only partner changes that were observed also occurred after the non-return of one

of the pair. Pairs generally remained faithful to a single breeding site although movements of up to 20m were observed.

Top breeders dominated the Wandering albatross breeding population and the differences in sample sizes between breeders of different quality made meaningful comparisons difficult. However, there did not appear to be any trend in the return rates of unsuccessful or successful breeders of different quality (Table 5.2).

Table 5.2
Overall breeding frequency in relation to breeding 'quality' (Section 4.3.8) of Wandering albatrosses on Macquarie Island (1994/95 - 2000/01)

		% breeding for next time in subsequent season					
Season	**Number of identified birds**	**1**	**2**	**3**	**4**	**5**	**6**
Successful breeders							
Top	52	0.0	95.7	3.0	0.0	0.0	0.0
Middle	11	0.0	100.0	0.0	0.0	0.0	0.0
Bottom [A]	2	-	-	-	-	-	-
Unsuccessful breeders							
Top	11	81.8	0.0	0.0	0.0	0.0	0.0
Middle	18	94.4	0.0	7.1	0.0	0.0	0.0
Bottom	14	71.4	14.3	0.0	0.0	0.0	0.0

[A] no successful bottom breeders were subsequently recorded breeding

5.3.2 Black-browed albatrosses

In contrast to the Wandering albatrosses, most Black-browed albatrosses bred annually and very few breeders deferred breeding for more than two seasons (Table 5.3). Unsuccessful breeders were more likely to defer breeding than successful breeders and this may in part be due to a successful breeding attempt reinforcing the pair bonds of successful pairs. Breeding frequency patterns were similar in each year for unsuccessful breeders; however, a lower proportion of successful breeders from 1999/00 returned to breed in 2000/01.

Breeding quality appeared to influence breeding frequency and some consistent trends were identified. *Top* quality unsuccessful breeders were most likely to defer breeding for one year

while bottom quality unsuccessful breeders were most likely to return to breed the following year. Similar proportions of successful *top* and *bottom* quality breeding birds returned to breed the following year; however, in a similar manner to unsuccessful birds, *top* quality breeders showed a greater tendency to defer breeding.

Table 5.3
Breeding frequency of Black-browed albatrosses in relation to breeding success (1994/95 - 2000/01)

		% breeding for next time in subsequent season						
Season	**Number of identified birds**	**1**	**2**	**3**	**4**	**5**	**6**	**Total**
Successful Birds								
1994/95	40	87.5	4.5	0.0	0.0	0.0	0.0	92.0
1995/96	43	86.0	12.2	0.0	0.0	0.0		98.2
1996/97	45	82.2	9.3	0.0	0.0			91.5
1997/98	31	93.5	3.4	0.0				97.0
1998/99	39	89.7	0.0					89.7
1999/00	38	68.4						68.4
Total	236	*84.3*	*5.1*	*0.0*	*0.0*	*0.0*	*0.0*	
Unsuccessful Birds								
1994/95	23	82.6	0.0	3.8	0.0	3.8	0.0	90.2
1995/96	26	80.8	0.0	3.7	0.0	0.0		84.5
1996/97	28	75.0	0.0	0.0	0.0			75.0
1997/98	46	82.6	0.0	0.0				82.6
1998/99	50	72.0	6.3					78.3
1999/00	44	77.3						77.3
Total	217	*77.9*	*6.4*	*1.6*	*0.0*	*2.0*	*0.0*	

The movements of nesting sites between successive breeding attempts by Black-browed albatrosses were also analysed. Out of 456 recorded breeding attempts, 109 (24%) were at a different location (i.e. greater than 10m) to the preceding attempt. Thirty-five percent of these were preceded by a gap of at least one season and most (75%) were preceded by an unsuccessful breeding attempt. Approximately two-thirds of breeding attempts following a location change were unsuccessful.

Table 5.4
Overall breeding frequency of Black-browed albatrosses on Macquarie Island in relation to breeding quality (1994/95 - 2000/01)

Season	Number of identified birds	% breeding for next time in subsequent season					
		1	2	3	4	5	6
Successful							
Top	103	90.3	6.8	0.0	0.0	0.0	0.0
Middle	60	78.3	5.6	0.0	0.0	0.0	0.0
Bottom	18	88.9	0.0	0.0	0.0	0.0	0.0
Unsuccessful							
Top	27	81.5	10.0	0.0	0.0	0.0	0.0
Middle	54	87.0	9.1	0.0	0.0	0.0	0.0
Bottom	67	92.5	3.7	2.6	0.0	0.0	0.0

5.3.3 Grey-headed albatrosses

Although most Grey-headed albatrosses showed a biennial breeding pattern when successful, the rate of deferral was high with approximately 18% of successful breeders overall deferring breeding for more than two years (Table 5.5). A small proportion of successful breeders also returned the following year to breed. The low proportion of successful breeders from 1997/98 returning to breed in 1999/00 could be attributable to missed pairs in the unusually late 1999/00 census.

Approximately 60% of unsuccessful breeders returned to breed the following year and a significant proportion of breeders also deferred breeding for one year after an unsuccessful breeding attempt. Although similar proportions of successful and unsuccessful breeders deferred breeding for more than two or one years respectively, comparatively few unsuccessful breeders deferred breeding for more than two years. A relatively low proportion of unsuccessful breeders from 1998/99 returned to breed in 1999/00 and like the successful breeders this is probably attributable to the late census of nests conducted in that season.

The relationship between breeding frequency of Grey-headed albatrosses and individual breeder quality is summarised in Table 5.6. *Middle* quality breeding birds (both successful and unsuccessful) showed the greatest adherence to the biennial breeding pattern.

Table 5.5
Breeding frequency of Grey-headed albatrosses in relation to breeding success (1994/95 - 2000/01)

Season	Number of identified birds	% breeding for next time in subsequent season						
		1	2	3	4	5	6	Total
Successful breeders								
1994/95	76	6.6	63.2	9.2	6.6	0.0	0.0	85.5
1995/96	96	4.2	64.6	8.3	2.1	1.0		80.2
1996/97	100	2.0	63.0	6.0	7.0			78.0
1997/98	80	2.5	36.3	28.8				67.5
1998/99	67	6.0	50.7					56.7
1999/00	53	0.0						0.0
Total	472	*3.6*	*56.3*	*12.5*	*5.1*	*0.6*	*0.0*	
Unsuccessful breeders								
1994/95	29	62.1	24.1	6.9	0	0	0	93.1
1995/96	42	81.0	11.9	0.0	0.0	0.0		92.9
1996/97	36	61.1	13.9	0.0	0.0			75.0
1997/98	50	74.0	14.0	0.0				88.0
1998/99	73	49.3	23.3					72.6
1999/00	42	38.1						38.1
Total	272	*59.9*	*17.8*	*1.3*	*0.0*	*0.0*	*0.0*	

Table 5.6
Overall breeding frequency in relation to breeding 'quality' (Section 4.3.8) of Grey-headed albatrosses on Macquarie Island (1994/95 - 2000/01)

Season	Number of identified birds	% breeding for next time in subsequent season					
		1	2	3	4	5	6
Successful							
Top	236	5.5	66.0	16.6	3.2	0.0	0.0
Middle	77	5.2	83.8	7.5	0.0	0.0	0.0
Bottom	27	3.7	43.5	23.8	15.8	0.0	0.0
Unsuccessful							
Top	48	56.3	26.2	3.3	0.0	0.0	0.0
Middle	68	82.4	10.9	0.0	0.0	0.0	0.0
Bottom	100	59.0	20.7	0.0	0.0	0.0	0.0

Both *top* and *bottom* quality unsuccessful breeders showed similar breeding frequency patterns while significantly more *bottom* quality successful breeders deferred breeding for three or four years after their last breeding attempt.

5.3.4 Light-mantled sooty albatrosses

The breeding frequency patterns of Light-mantled sooty albatrosses (all sites pooled) are summarised in Table 5.7. Although most unsuccessful breeders returned to breed the following season, over 25% missed at least one season before returning to breed.

Table 5.7
Breeding frequency of Light-mantled sooty albatrosses in relation to breeding success (all sites pooled, 1994/95 - 2000/01)

		% breeding for next time in subsequent season						
Season	**Number of identified birds**	**1**	**2**	**3**	**4**	**5**	**6**	**Total**
Successful breeders								
1994/95	122	0.8	62.3	7.4	7.4	0.8	2.5	81.1
1995/96	111	0.0	59.5	3.6	6.3	3.6		73.0
1996/97	132	1.5	65.9	2.3	10.6			80.3
1997/98	141	0.0	61.0	9.2				70.2
1998/99	141	0.0	56.0					56.0
1999/00	84	2.4						2.4
Total	731	*0.7*	*60.9*	*5.7*	*8.2*	*2.1*	*2.5*	
Unsuccessful breeders								
1994/95	111	45.0	20.7	10.8	0.9	0.0	1.8	79.3
1995/96	137	58.4	14.6	4.4	3.6	1.5		82.5
1996/97	193	60.1	10.9	7.8	5.7			84.5
1997/98	132	62.1	14.4	3.8				80.3
1998/99	129	42.6	20.2					62.8
1999/00	111	73.0						73.0
Total	813	*57.1*	*15.5*	*6.6*	*3.9*	*0.8*	*1.8*	

Breeding frequency patterns were relatively similar from 1994/95 to 2000/01, particularly for successful breeders. There was more variation in the return rates of unsuccessful breeders and comparatively few unsuccessful breeders from 1994/95 and 1998/99 returned to breed the

following year. In both cases the number of breeders that returned the year after was comparatively high.

The overall breeding frequency rates at each of the breeding success sites used in these analyses are shown in Table 5.8. Even though the proportion of birds deferring breeding appeared variable at the different sites (e.g. n+1 –50% Bauer Bay cf 70% Gadget and First Gullies) no significant differences were found in the return rates of successful (Two-way ANOVA, F_4=1.0, p=0.45) or unsuccessful breeders (Two-way ANOVA, F_4=0.6, p=0.65) at the different locations. Return rates at Bauer Creek differed from other sites in that no successful breeders deferred breeding for more than two seasons. It is also noteworthy that the two sites with the lowest return rates of unsuccessful breeders (Hurd Point and Lusitania Bay) also had the highest overall breeding success of the five sites (see Chapter 4).

Table 5.8
Overall breeding frequency of Light-mantled sooty albatross at five breeding success sites (1994/95 - 2000/01)

		% breeding for next time in subsequent season					
Season	**Number of identified birds**	**1**	**2**	**3**	**4**	**5**	**6**
Successful breeders							
Gadget and 1st	101	0.9	69.5	9.0	1.6	2.3	9.4
Bauer Creek	24	0.0	50.0	12.5	0.0	0.0	0.0
Sandy Bay	148	0.7	64.3	7.4	3.4	0.0	0.0
Hurd Point	192	1.6	57.1	6.3	15.9	2.3	-
Lusitania Bay	262	0.0	59.2	2.2	9.5	3.1	0.0
Unsuccessful breeders							
Gadget and 1st	150	64.9	17.0	6.3	0.0	1.9	0.0
Bauer Creek	205	56.1	17.6	8.8	1.9	1.6	0.0
Sandy Bay	205	55.6	13.8	5.4	7.2	0.0	2.6
Hurd Point	98	54.1	10.6	4.0	3.4	0.0	-
Lusitania Bay	97	48.5	17.2	9.0	6.0	0.0	4.3

The breeding frequencies of Light-mantled sooty albatrosses of differing breeding quality were also compared (Table 5.9). The proportion of successful and unsuccessful breeders that

followed the biennial breeding pattern was high compared to the overall breeding frequency patterns of the pooled data with all breeders. It appears likely that breeders that have only had one or two sporadic breeding attempts between 1994/95 and 2000/01 heavily influenced the overall breeding frequency data.

Table 5.9
Overall breeding frequency in relation to breeding 'quality' (Section 4.3.8) of Light-mantled sooty albatrosses on Macquarie Island (1994/95 - 2000/01)

		% breeding for next time in subsequent season					
Season	**Number of identified birds**	**1**	**2**	**3**	**4**	**5**	**6**
Successful breeders							
Top	348	0.9	81.8	7.3	8.1	1.0	0.0
Middle	85	0.0	84.3	8.9	0.0	0.0	0.0
Bottom	62	0.0	70.9	7.3	0.0	5.0	0.0
Unsuccessful breeders							
Top	85	71.8	22.7	3.8	2.7	0.0	0.0
Middle	95	84.2	12.8	4.3	0.0	0.0	0.0
Bottom	406	69.7	17.7	5.3	5.3	0.0	0.0

Bottom quality successful breeders were less likely to return to breed after missing one season than the top or middle quality successful breeders and while *top* quality breeders showed similar return rates to middle quality breeders after one year, significantly more successful top breeders returned to breed after three seasons. Unsuccessful breeders showed a similar pattern to the successful breeders with bottom breeders again showing the lowest rates of return in the year following a successful breeding attempt and top unsuccessful breeders were more likely to return to breed after missing one or more seasons.

5.3.5 Partner changes

Wandering albatrosses showed the least inclination to change partners between breeding attempts and any partner changes that were recorded only occurred after the non-return of a mate. Therefore no data from this species are included in the following analyses. Black-browed albatrosses were the most likely to change partner with 8% of breeding attempts occurring with a different partner to the previous attempt (Table 5.10).

In contrast, less than half of all Black-browed partner changes were preceded by a break of more than one season, which is probably due in part to the annual breeding nature of this species.

Table 5.10
Number of partner changes of Black-browed, Grey-headed and Light-mantled sooty albatrosses between successive breeding attempts (1994/95 and 2000/01)

Species	Number breeding attempts	Overall partner changes		Partner change preceded by gap > 1 season		Success of previous breeding attempt		Resultant success after partner change	
		n	%	n	%	%s	%u	%s	%u
Black-browed albatross	456	36	7.9	16	44.4	33.3	66.7	27.8	72.2
Grey-headed albatross	752	38	5.1	38	100.0	68.4	31.6	65.8	34.2
Light-mantled sooty albatross	1489	48	3.2	36	75.0	50.0	50.0	52.1	47.9

%s - percentage successful, %u - percentage unsuccessful

Almost two-thirds of Grey-headed partner changes were preceded by a successful breeding attempt suggesting that most partner changes were in response to the non-return of a partner. In contrast, only one-third of Black-browed partner changes were preceded by a successful breeding attempt. Grey-headed albatrosses also tended to have more successful breeding attempts following a partner change while only one-third of Black-browed albatrosses breeding attempts were successful following a partner change. Light-mantled sooty albatrosses showed a different pattern to both these species with partner changes preceded by very similar proportions of successful and unsuccessful breeding attempts. The success of a Light-mantled sooty albatross breeding attempt following a partner change was also evenly divided between successful and unsuccessful results.

5.3.6 Breeding frequency and the timing of failure

The timing of failure appeared to have little effect on the breeding frequency of the annually breeding Black-browed albatrosses (Figure 5.1). However, the timing of failure clearly influenced the return rates of the biennially breeding Grey-headed and Light-mantled sooty albatrosses (Figures 5.2 and 5.3). Unsuccessful Grey-headed albatrosses tended to return the following year to breed if failures occurred before day 140 (two month old chick); however, no breeders returned the following year if failures occurred after 140 days post laying. Similar results were observed for Light-mantled sooty albatrosses, and no breeders returned to breed the following year if the nest failure occurred after late February (again, equivalent to a two month old chick). In contrast to the Grey-headed albatrosses where there appeared to be a distinct cut off point, return rates of Light-mantled sooty albatrosses gradually decreased with later failures. A significant negative correlation was found between the timing of Light-mantled sooty albatross failures and the proportion of breeders that returned the following year (Spearmans Rank, $r^s_9 = -0.91$, $p=0.001$).

It was not possible to conduct similar analyses with the Wandering albatrosses due to the infrequent occurrence of late failures. The latest recorded failure and subsequent return of the pair the following year occurred in May when the chick was just over two months old. Failures before this invariably resulted in the breeding birds returning the following year to breed. However, it is unlikely that breeders failing after this time would return to breed the following year.

Figure 5.1
Influence of timing of failure on breeding frequency of Black-browed albatrosses

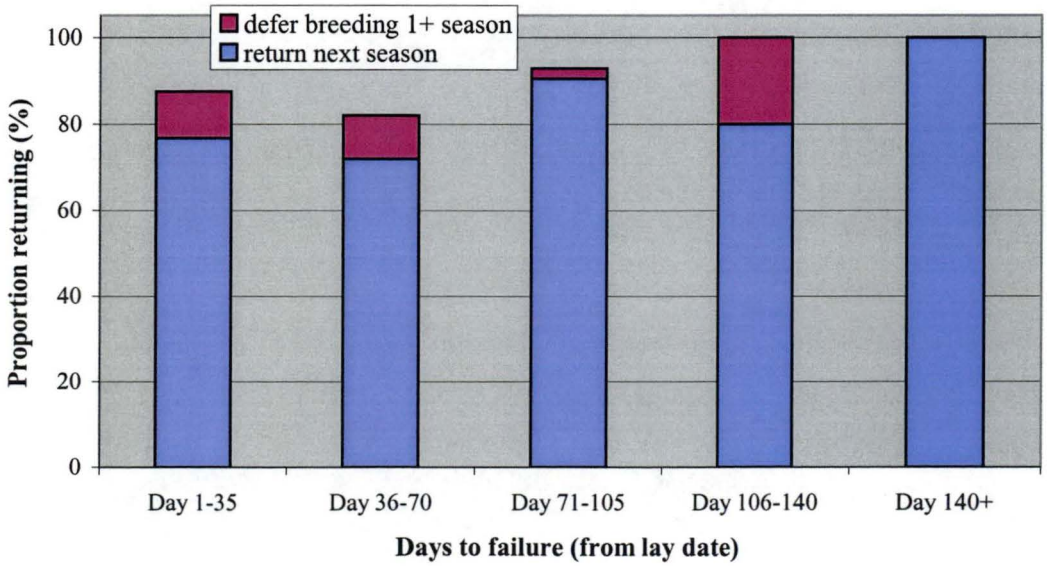


Figure 5.2
Influence of timing of failure on breeding frequency of Grey-headed albatrosses

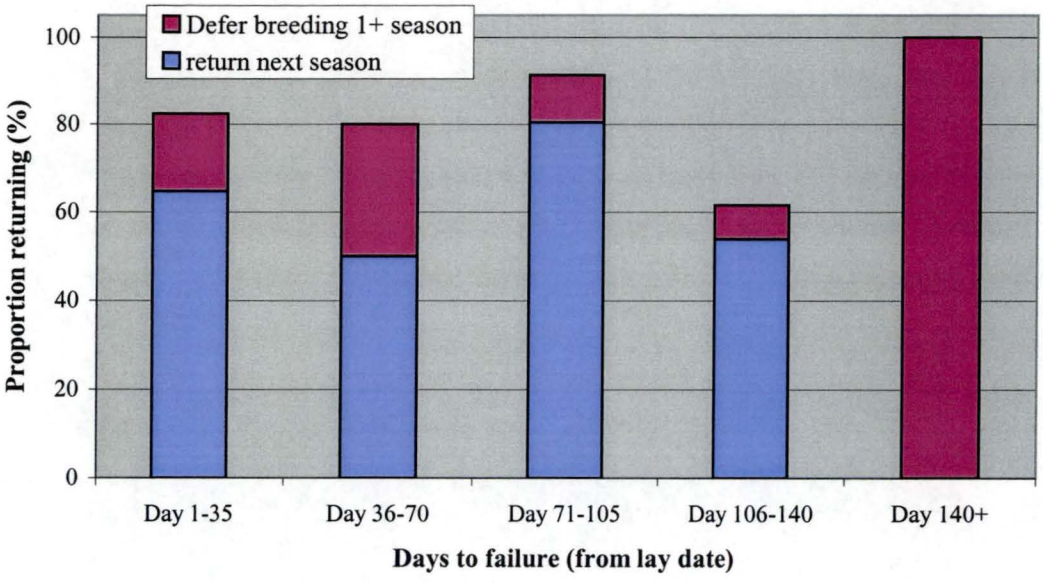
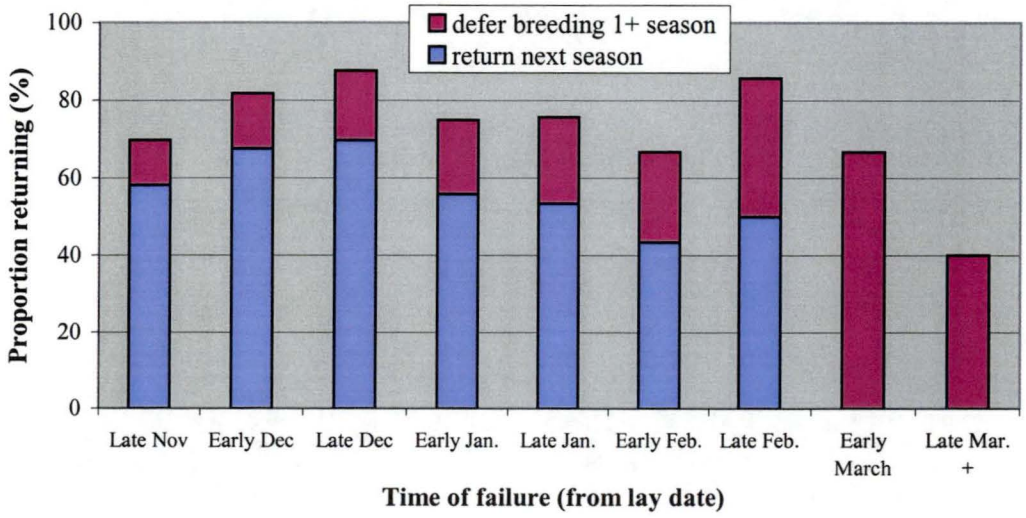


Figure 5.3
Influence of timing of failure on breeding frequency of Light-mantled sooty albatrosses



5.3.7 Biases in the data

To confidently determine breeding frequency patterns it is fundamental that all breeding pairs are recorded each year and comprehensive datasets have been obtained for the Wandering, Black-browed and Grey-headed albatrosses. These datasets are unique in that they represent the entire breeding populations, rather than sub-samples of populations used in other studies (Jouventin and Weimerskirch 1988; Croxall 1991; Prince *et al.* 1994; Waugh *et al.* 1999b). Relatively few breeders of these species were not identified each season and as a result the data are likely to accurately reflect the breeding frequency patterns. The 1999/00 season was an exception as we arrived late on Macquarie Island when a significant proportion of the Black-browed and Grey-headed albatross nests had already failed. Most Black-browed albatross pairs that had already failed were identified and the data are comparable with previous seasons. However, ten failed Grey-headed albatross nests were identified without identifying the breeders. This is reflected in the data with unusually low return rates for successful Grey-headed albatrosses from 1997/98 and unsuccessful birds from 1998/99.

There is more potential for bias in the Light-mantled sooty albatross data. Firstly, while the sample size of breeding birds was relatively large, unlike the other species it is only a sub-sample and does not cover the entire breeding population. Therefore it is possible that birds have returned and bred just outside the breeding success sites and were not found. However, this issue has been addressed in other studies on albatross breeding frequency (e.g. Croxall *et al.* 1990; Prince *et al.* 1994) where it was found to have a negligible effect if the sample size was sufficiently large.

5.4 DISCUSSION

5.4.1 Inter-species comparisons

The breeding frequency pattern of each species was documented between 1994/95 and 2000/01. Wandering albatrosses exhibited a typical biennial breeding pattern with 90% of successful breeders returning to breed two seasons later. A lower proportion of unsuccessful Wandering albatrosses returned to breed the following year (~84%); however this deferral was almost invariably linked to the non-return of a partner. The low number of partner changes observed between 1994/95 and 2000/01 may be partly attributable to the small sample size; however the strength of the pair and nest bonds (often formed in the two to three years prior to the first breeding attempt) are also likely to play a significant role.

Grey-headed and Light-mantled sooty albatrosses also showed a consistently biennial breeding pattern; however, there was considerably more deferral of breeding compared to Wandering albatrosses. Approximately 75% of Grey-headed albatrosses that deferred breeding did so for only one extra season while Light-mantled sooty albatrosses often deferred for two or three seasons. Both Grey-headed and Light-mantled sooty albatrosses showed similar levels of partner change and most were preceded by a break of more than one season. The timing of failure also influenced the return rates of unsuccessful breeders of these two species. Failures that occurred after the chick was approximately two months old generally precluded the return of that breeding pair the following season.

Black-browed albatrosses showed a typically annual breeding pattern that did not appear to be influenced by the timing of failure. This species also showed the most proclivity to change partners or locations and this could be due to the weakness of pair bonds that are often quickly formed as part of the pre-breeding interactions between birds. Failed breeding attempts appear to have a bigger impact on the pair or nest bond of this species, and most partner changes or location changes appeared to be in response to a failed breeding attempt.

5.4.2 Comparisons with other locations

A comparison of breeding frequency data from five subantarctic breeding sites is summarised in Table 5.11. More successful Wandering albatrosses at Bird Island, South Georgia deferred breeding in comparison to the breeding populations on Iles Crozet and Macquarie Island. These lower return rates after two seasons at Bird Island may be due in part to missed breeders in the initial census and when a correction factor was applied to account for this, 72% of breeders were estimated to follow a biennial breeding pattern (Appendix 1 in Croxall *et al.* 1990). Differences between locations may reflect differences in the foraging ecology of the two species as discussed in Chapters 3 and 4. Unsuccessful breeders also showed a higher deferral of breeding at Bird Island. It is possible this difference is related to differences in the contribution of hatching and chick success to breeding success at the different locations. Chick success was considerably lower at Bird Island compared to Macquarie Island (Chapter 4, Croxall *et al.* 1998) and therefore higher rates of deferral might be expected at Bird Island.

The breeding frequency of Black-browed albatrosses was very similar at all locations and this is probably attributable to the annual breeding pattern of this species.

Table 5.11
Comparison of mean breeding frequency data from Wandering, Black-browed, Grey-headed, Light-mantled sooty albatrosses and similar conspecifics breeding at Macquarie Island, Bird Island, Iles Crozet, Iles Kerguelen and Campbell Island

Location	Time frame	N	% breeding for next time in subsequent season (mean[A])				Reference
			1	2	3	4+	
Successful breeders							
Wandering albatrosses (*Diomedea exulans*)							
Macquarie Island	1994-2000	74	0	89	4	0	this study
Bird Island[B]	1976-1985	2170	0	66 (72)	13 (8)	7 (6)	Croxall *et al*. 1990
Iles Crozet	Unknown	?	0	89	6	4	Jouventin and Weimerskirch 1988
Black-browed albatrosses (*Thalassarche melanophrys*)							
Macquarie Island	1994-2000	236	85	6	0	0	this study
Bird Island	1976-1987	2468	81	7	3	1	Prince *et al.* 1994
Campbell albatrosses (*Thalassarche impavida*)							
Campbell Island	1991-1994	301	83	7	1	1	Waugh *et al.* 1999
Grey-headed albatrosses (*Thalassarche chrysostoma*)							
Macquarie Island	1994-2000	472	4	56	13	6	this study
Bird Island	1976-1987	3421	1	68	11	7	Prince *et al.* 1994
Light-mantled sooty albatrosses (*Phoebatria palpebrata*)							
Campbell Island	1991-1994	253	2	62	8	7	Waugh *et al.* 1999
Light-mantled sooty albatrosses							
Macquarie Island	1994-2000	731	1	61	6	10	this study
Posession Island	Unknown	?	0	75	12	3	Jouventin and Weimerskirch 1988
Unsuccessful breeders							
Wandering albatrosses (*Diomedea exulans*)							
Macquarie Island	1994-2000	45	90	4	0	12	this study
Bird Island[B]	1976-1985	1655	63 (68)	17	8	-	Croxall *et al.* 1990
Iles Crozet	Unknown	?	84	10	3	2	Jouventin and Weimerskirch 1988
Black-browed albatrosses (*Thalassarche melanophrys*)							
Macquarie Island	1994-2000	217	78	1	2	2	this study
Bird Island	1976-1987	1489	75	9	3	1	Prince *et al.* 1994
Campbell albatrosses (*Thalassarche impavida*)							
Campbell Island	1991-1994	83	74	8	1	1	Waugh *et al.* 1994
Grey-headed albatrosses (*Thalassarche chrysostoma*)							
Macquarie Island	1994-2000	272	61	17	2	0	this study
Bird Island	1976-1987	3524	54	23	5	3	Prince *et al.* 1994
Campbell Island	1991-1994	324	72	13	3	2	Waugh *et al.* 1994
Light-mantled sooty albatrosses (*Phoebatria palpebrata*)							
Macquarie Island	1994-2000	813	57	16	7	4	this study
Posession Island	Unknown	?	59	25	12	3	Jouventin and Weimerskirch 1988

[A] - mean values for Macquarie Island are cited hear to facilitate comparisons with the other studies (overall values in text)

[B] - values in parentheses have been adjusted to take into account a variable recapture rate and therefore correct for birds that may have been missed

Jouventin and Weimerskirch (1988) suggested that the shorter breeding cycle and tendency of this species to forage in near shore productive waters were significant factors in the maintenance of an annual breeding cycle. It seems likely that these factors are also responsible for the similarity in breeding frequency observed at the different breeding sites.

Grey-headed albatrosses also showed similar patterns of breeding frequency at the three subantarctic breeding sites, with the Bird Island population showing the highest rate of return after two seasons and Macquarie Island breeders the highest deferral rate. Macquarie Island also had a higher proportion of successful Grey-headed albatrosses returning the following year to breed. Croxall (1991) suggested that successful females were physiologically unable to return to breed in the year following a successful breeding attempt and that males (returning to breed with different females) comprised the entire proportion of breeders that showed this pattern. The return of established successful pairs in successive years was noted in the present study showing that it is possible, under some circumstances, for successful female Grey-headed albatrosses to breed in successive years. Hector *et al.* (1986) suggested that Grey-headed albatrosses were inherently annual breeders, and some environmental factor associated with breeding successfully caused the ovary to secrete progesterone instead of oestrogens. This was not evident in a very small proportion (~4%) of female Grey-headed albatrosses breeding on Macquarie Island. In all studies, for both Black-browed and Grey-headed albatrosses, significant variation in breeding frequency was observed between years and such variation may be largely attributable to fluctuations in available food resources and the ability of a pre-breeding bird to acquire adequate condition (Prince *et al.* 1994; Croxall *et al.* 1998; Waugh *et al.* 1999a; Waugh *et al.* 1999b).

There are few published data on the breeding frequency of Light-mantled sooty albatrosses. The only other comprehensive multi-year published study on the breeding frequency of this species was described by Jouventin and Weimerskirch (1988) for the population on Possession Island, Iles Crozet. These authors found 71% of successful breeders returned two seasons after a breeding attempt while only 61% were found to follow this strategy on Macquarie Island. There was also a greater tendency for successful Light-mantled sooty albatrosses from Macquarie Island to defer breeding for more than four seasons relative to birds on Possession Island (Jouventin and Weimerskirch 1988). The return rates of unsuccessful breeders from the two locations were more similar although more breeders from Possession Island were resighted overall. In an earlier study on Light-mantled sooty albatrosses from Macquarie Island, Kerry and Garland (1984) suggested that 30% of successful Light-mantled sooty albatrosses on Macquarie Island returned to breed after missing one season and 18% of successful breeders returned after missing two seasons. These

authors also found that 33% of failed breeders returned the following years. The differences between the two studies are likely to be attributable to differences in methodology and the intensity of searches of discrete areas in successive years. Accurate assessment of breeding frequency require comprehensive counts of breeding birds in the same areas for several successive seasons and without these details on the latter study it is not possible to establish the comparability of the breeding frequency estimates.

5.4.4 Breeding frequency and individual breeder quality

Few studies have examined the breeding frequency of albatrosses in the context of individual breeder quality. Due to the predominance of *top* quality breeding birds in the Wandering albatross population on Macquarie Island, it was not possible to ascertain the effect of individual breeding quality on breeding frequency. Trends in return rates of the other species were mixed. *Top* quality Black-browed albatrosses showed a greater ability to defer breeding although there was little variation between the annual return rates of birds of different breeding quality. This may reflect the ability of *top* quality breeding birds to 'decide' not to breed in seasons that are less conducive to successful breeding. There were also significant differences in the return rates of Grey-headed albatrosses of different breeding quality. Successful breeding birds of *low* quality were the least likely to breed biennially and a high proportion deferred breeding for three or four seasons. The high proportion of *middle* quality breeders that followed a typical biennial breeding pattern seems anomalous and the mechanisms underlying the differences between the return rates of breeders of different quality are unclear. This pattern was also observed with the Light-mantled sooty albatross although the differences between *middle* and *top* quality breeders were not as pronounced relative to Grey-headed albatrosses.

It appears that while individual breeding quality influenced breeding frequency to some degree, there are few consistent trends between species. There was some evidence that *top* breeders have a greater ability to defer breeding and this is likely to be in response to environmental cues in the non-breeding season.

5.4.5 Partner changes and movements of nest sites

The likelihood of changing partners was not consistent between species. Wandering albatrosses usually spend two or three year's pair and nest bonding before breeding, and are the least likely to change partners. Light-mantled sooty albatrosses also rarely change partners, and when changes did occur, most were preceded by a break of at least one season from the previous breeding attempt. All partner changes by Grey-headed albatrosses were

preceded by a gap of at least one season, most were preceded by a successful breeding attempt and most breeding attempts with a new partner were successful. Relatively few Black-browed albatrosses that had established a pair bond and bred successfully changed partners, however, some established pairs moved their nest site between breeding attempts. Unsuccessful Black-browed albatrosses were three times as likely to change partner than successful breeders and this is probably attributable to the lack of any well-established pair or nest bond. Qualitative observations suggest that some birds have inherent difficulties in forming pair bonds or nest bonds and as a result breed unsuccessfully for several consecutive years, often with different partners.

The number of partner changes in all species increased with time from last breeding attempt increased. This suggests that most of these partner changes were caused by the non-return of a partner, which may have important implications for survivorship. The above results provide circumstantial evidence of the relative strength of the pair and nest bond, and this appears to be closely linked breeding frequency and other aspects of life history such as age at first breeding, survivorship and foraging ecology.

Although the sample size was small it is clear that Wandering albatrosses have the strongest pair and nest bond, and as previously noted, this is attributable to the pair and nest bonding usually undertaken in the years preceding the first breeding attempt (Pickering 1989). Grey-headed and Light-mantled sooty albatrosses generally do not start breeding until 10-11 years of age (This study, Jouventin and Weimerskirch 1988; Prince *et al.* 1994; Waugh *et al.* 1999b) and this may allow time for stronger pair bonds to form prior to breeding. However, the breeding success of these species did not appear to be negatively influenced by a partner change and this may be evidence of an inherent ability to rapidly form strong pair bonds. Croxall (1991) suggested that Grey-headed albatrosses visited breeding colonies in the non-breeding season to renew pair bonds and confirm that their partners were still alive. Both Grey-headed and Light-mantled sooty albatrosses have been observed behave in this way on Macquarie Island and such behaviour would also facilitate partner changes after the non-return of a mate.

The relatively high rate of partner and location changes amongst Black-browed albatrosses probably reflects weaker pair and nest bonds that were formed more rapidly. Factors that are primarily responsible for this include aggressive responses to unsuccessful breeding attempts, a lower age at first breeding and relatively quick turnaround time between breeding attempts.

5.4.6 The evolution of breeding frequency

In evolutionary terms it is likely that the differences in breeding frequency of the four albatross species under investigation are inextricably linked to the ability of a species to fledge a chick in a prescribed time frame, which in turn is closely tied to body size, foraging ecology and provisioning strategy (Jouventin and Weimerskirch 1988). For example, Prince (1985) showed that the composition and energy content of the diet might be significant factors in the different breeding strategies observed in Grey-headed and Black-browed albatrosses, and such factors are almost entirely dependent on the foraging strategy of a species. Physiological processes also play an important role (Hector *et al.* 1985; Hector *et al.* 1986) and are also closely linked to behavioural and ecological influences (Croxall 1991).

Black-browed albatrosses tend to be more neritic feeders (Prince *et al.* 1998; Waugh *et al.* 1999a; Waugh *et al.* 2000; Chapter 7), have the shortest mean foraging trips (Tickell and Pinder 1975; Huin *et al.* 2000, Chapter 6) and are capable of fledging a chick more rapidly than the other two smaller albatrosses breeding on Macquarie Island (Huin *et al.* 2000; Chapter 6). These factors are fundamental to the maintenance of the annual breeding pattern. Grey-headed albatrosses generally forage in more distant waters (Prince *et al.* 1998; Waugh *et al.* 1999a; Waugh *et al.* 2000; Nel *et al.* 2000; Chapter 7), have significantly longer foraging trips and take longer to fledge a chick (Tickell and Pinder 1975; Huin *et al.* 2000, Chapter 6). Incubating Light-mantled sooty albatrosses forage primarily south of the convergence (Weimerskirch and Robertson 1994), have the longest mean shift length (Chapter 6) and also take a relatively long time fledge a chick (Chapter 8). It is likely that the disparity in the deferral of breeding between Black-browed, Grey-headed and Light-mantled sooty albatrosses can be largely attributed to the above factors. Studies have also shown that species that forage primarily in pelagic waters are more likely to defer breeding in response to body condition than those feeding in neritic waters (Chaurand and Weimerskirch 1994a; Chastel 1995).

The cost of breeding and foraging appears to be a real factor in the variation observed in breeding frequencies of the smaller albatrosses on Macquarie Island. The similarity in the breeding frequency patterns of Grey-headed and Light-mantled sooty albatrosses observed here is likely to be associated with the similar life history attributes of these species, particularity their tendency to forage in more pelagic waters. Prince *et al.* (1994) suggested that any fundamental demographic differences between annual and biennial breeding species should be most evident with species of similar size breeding sympatrically, and this was evident in the current study. The rate of return of Wandering albatrosses does not appear to be

influenced by the cost of breeding (this study, Weimerskirch 1992a) and their large size is likely to be a major factor in its biennial breeding strategy (Jouventin and Weimerskirch 1988; Croxall 1991).

Chapter 6 - The attendance patterns of albatrosses on Macquarie Island during the incubation and brood-guard periods

6.1 INTRODUCTION

Attendance patterns are inextricably linked to the foraging strategies of Procellariiformes and studies into these patterns can give insight into the distances travelled and areas utilised by each species (Lack 1968; Ashmole 1971). The breeding and foraging grounds of most albatrosses are typically separated and shift lengths during incubation and the brood guard stage are related to the time of the breeding cycle, distance to foraging areas, body size and fasting ability (Warham 1990). The larger eggs of Procellariiformes, particularly albatrosses, take a relatively long time to hatch (in the order of 65-80 days), and therefore attendance patterns need to be strictly regulated in order to successfully incubate an egg to hatching. Chick rearing is also extended and ranges from four to nine months in albatrosses (Warham 1990). Extended breeding seasons of this nature require foraging regimes that allow breeders to spend a significant amount of time on the egg whilst incubating, supply sufficient food to the chick during the brood-guard stage and still maintain their own condition throughout the breeding cycle.

Most albatrosses forage primarily in neritic or pelagic waters; however, many utilise a combination of both depending on the stage of the breeding cycle (e.g. Weimerskirch 1998; Prince *et al.* 1999). The principal foraging strategy utilised by a species can also be linked to the location of the breeding population and the available food resources (Prince *et al.* 1998; Waugh *et al.* 1999a). Species that feed primarily in neritic waters (e.g. Black-browed (*Thalassarche melanophrys, T. impavida*) and Shy albatrosses (*T. cauta*)) often target the high productivity associated with the continental shelf or undersea ridges (Brothers *et al.* 1998; Waugh *et al.* 1999a; Hedd *et al.* 2001). Consequently the shift lengths of these species are often shorter as the distances travelled during foraging are not as great. Other species such as Grey-headed albatrosses (*T. chrysostoma*) target pelagic frontal zones as their main source of food (Waugh *et al.* 1999a; Nel *et al.* 2001) and consequently shift lengths of such species are generally longer (Tickell and Pinder 1975).

Satellite telemetry studies have also shown that Wandering albatrosses (*Diomedea exulans*) cover vast areas in search of suitable foraging grounds and that males and females often target different areas (e.g. Weimerskirch *et al.* 1993; Weimerskirch 1995; Prince *et al.* 1998). Light-mantled sooty albatrosses (*Phoebetria palpebrata*) also cover vast distances during the

breeding cycle and generally target areas south of the Antarctic Convergence (Weimerskirch and Robertson 1994; Weimerskirch 1998). Such foraging strategies generally result in longer mean shift length during the breeding cycle of these species (Weimerskirch *et al.* 1986; Weimerskirch 1995).

Although there have been a number of studies on the foraging routine of many breeding procellariiform species after the brood-guard stage (e.g. Chaurand and Weimerskirch 1994b; Weimerskirch *et al.* 1994a; Weimerskirch *et al.* 1997c; Catard *et al.* 2000; Duriez *et al.* 2000; Huin *et al.* 2000; Phillips and Hamer 2000; Waugh *et al.* 2000) there are relatively few data on the attendance patterns of albatrosses prior to the chick being left unattended. The attendance patterns of Black-browed and Grey-headed albatrosses were documented on Bird Island, South Georgia in the 1970's (Tickell and Pinder 1975) and Weimerskirch *et al.* (1986) described the attendance patterns of six albatross species (Wandering, Black-browed, Grey-headed, Yellow nosed (*T. carteri*) and the two sooty albatrosses (*Phoebetria palpebrata* and *P. fusca*) breeding at Iles Crozet. The attendance patterns of Shy albatrosses were comprehensively documented by Hedd (1999) and the incubation routine of Wandering albatrosses was described by Weimerskirch (1995).

There are even fewer data on the attendance patterns during the incubation and brood/guard stage of the albatrosses breeding on Macquarie Island. The attendance patterns of non-breeding Wandering albatrosses were documented by Tomkins (1985a) in 1975/76 and 1976/77; however, there are no other published data on the attendance patterns of albatrosses breeding on Macquarie Island. This chapter describes the attendance patterns of all albatross species on Macquarie Island and examines these patterns in the context of individual breeder quality and breeding success.

6.1.2 Research questions

1. What are the attendance patterns of the albatross species on Macquarie Island during the incubation and brood-guard stages and are they indicative of broad trends in foraging ecology ?

2. Are there any correlations between these attendance patterns and individual breeder quality (as defined in Chapter 4, Sections 4.2.3 and 4.3.8)

3. Is there a relationship between mean shift length and breeding success ?

6.2 DATA PROCESSING AND ANALYSES

Shift lengths were obtained during the incubation and brood-guard stages using daily observations of marked birds (Wandering, Black-browed and Grey-headed albatrosses) and VHF transmitters (Light-mantled sooty albatrosses). Four categories of shift length were examined:

1. early incubation – laying to half way through incubation
2. late incubation – half way through incubation to the last shift preceding hatching
3. hatching – the shift in which the egg hatched
4. brood-guard – post hatching shift to chick fully unattended.

Shift lengths obtained via daily observations were accurate to ± 12 hours while shift lengths obtained using VHF transmitters were accurate to ± one hour. Daily observations were conducted concurrently with the Automatic Tracking System during 1999/00 and 2000/01 on Light-mantled sooty albatrosses and the differences were found to be negligible (One-way ANOVA, $f_{11} = 1.10$, $p=0.37$).

Mean shift lengths (± s.e) of each category were calculated for each species for each year. In 1999/00 and 2000/01, birds carrying satellite transmitters were excluded from the analyses to ensure that all shifts were comparable. Data were also pooled across years and mean values calculated for each category. Non-parametric statistical tests were used to test for differences between categories and years, as the data were not normally distributed (Zar 1974). The shift lengths of *top* quality (successful on two-thirds of breeding attempts) or *bottom* quality (unsuccessful on two-thirds of breeding attempts) breeding birds as (defined in Sections 4.2.3 and 4.2.8) were also examined and compared using non-parametric statistical tests. This was only done for Black-browed and Grey-headed albatrosses due to the paucity of data on Wandering albatross breeders of *bottom* quality and the small sample size of Light-mantled sooty albatrosses (in terms of both quality and shift data). Spearman Rank Correlation Tests (Zar 1974) were also used to test for relationships between mean shift length and breeding success.

6.3 RESULTS

6.3.1 Incubation, brood guard and fledging periods

Incubation periods, brood-guard periods and age at fledging of all four albatross species were determined as part of the investigation into attendance patterns and these data are summarised

in Table 6.1. The incubation periods of Wandering albatrosses were consistent ranging from 78-81 days with an overall mean of 79.2 ± 0.2 (s.e) days. The incubation periods of Black-browed and Grey-headed albatrosses were shorter with overall means of 69.2 ± 0.2 days and 71.7 ± 0.1 days respectively. Light-mantled sooty albatrosses had the shortest incubation period (mean - 66.5 ± 0.3 days). The incubation periods of Light-mantled sooty albatrosses were only recorded for one year and consequently the sample size was considerably smaller.

Table 6.1
Summary of incubation, brood guard and fledgling periods (in days) of the albatrosses breeding on Macquarie Island from 1994/95 to 2000/01

Species	Stage	Mean	s.e	n	min	max
Wandering albatross	Incubation	79.2	0.2	32	78	81
	Brood-guard	30.1	0.8	15	25	35
	Fledge	273.6	3.6	27	251	330
Black-browed albatross	Incubation	68.9	0.2	103	66	74
	Brood-guard	22.4	0.5	98	11	32
	Fledge	118 [A]	-	27	110	127
Grey-headed albatross	Incubation	71.7	0.1	104	67	75
	Brood-guard	24.8	0.3	93	16	32
	Fledge	135 [A]	-	15	128	143
Light-mantled sooty albatross	Incubation	66.5	0.3	12	65	68
	Brood-guard	19.9	0.4	29	16	24
	Fledge	139.7	2.6	6	133	151

[A] median values

Brood-guard periods were more variable and a similar hierarchy to incubation periods was observed with Wandering albatrosses having the longest brood guard, followed by the Grey-headed, Black-browed and Light-mantled sooty albatrosses. Fledging times also followed a similar pattern with Light-mantled sooty albatrosses fledging a chick in the shortest time, and Wandering albatrosses the longest. No mean values of fledging time were obtained for Black-browed and Grey-headed albatrosses, as observations were too infrequent to determine the

precise fledgling date. The median values in Table 6.1 were calculated from ranges that were less than five days in length.

No significant differences were observed between years for any of the incubation or brood guard periods with the exception of the brood-guard stage of Black-browed albatrosses (One-way ANOVA, $F_5=7.8$, $p<0.001$). Post-hoc tests (Tukey HSD) indicated that these differences were attributable to significantly longer mean brood-guard stages in 1996/97 and 1997/98 and a significantly shorter mean brood-guard stage in 1999/00.

6.3.2 Shift length

6.3.2.1 Mean shift length, between species variation and inter-annual variation

All shift data collected from the four albatross species on Macquarie Island between 1994/95 and 2000/01 are contained in Appendix 6.1 and summary values are contained in Table 6.2. These data are further summarised in Figures 6.1-6.4.

Table 6.2
Mean shift lengths for Wandering, Black-browed, Grey-headed and Light-mantled sooty albatrosses on Macquarie Island from 1994/95 to 2000/01

Species	early incubation			late incubation			hatch			brood/guard		
	mean	s.e	n	mean	s.e	n	mean	s.e	n	mean	s.e	n
Wandering albatrosses	8.8	0.44	196	8.8	0.34	210	6.6	0.59	33	3.1	0.10	229
Black-browed albatross	3.1	0.08	947	3.6	2.70	660	3.4	0.25	110	1.7	0.03	1283
Grey-headed albatross	5.0	0.19	321	7.5	0.22	320	5.6	0.28	112	2.5	0.06	902
Light-mantled sooty albatross				10.5	0.42	122	6.3	0.45	28	2.1	0.07	268

Black-browed albatrosses had the shortest mean shifts during incubation, followed by the Grey-headed, Light-mantled sooty and Wandering albatrosses. The mean shift lengths of the four species during the brood-guard stage were more similar and consistent both within and

between years. The mean brood-guard shift length was significantly shorter than mean shift length during both early and late incubation for all species (Table 6.3). There was no significant difference between early and late incubation in Wandering albatrosses; however, shift lengths of both Black-browed and Grey-headed albatrosses in early incubation were significantly shorter than in late incubation (Table 6.3).

Table 6.3
Summary of statistical tests (Mann-Whitney U) comparing mean shift lengths (pooled data) of albatrosses on Macquarie Island (1994/95 - 2000/01)

Species	Comparision	Z	p-value
Wandering albatross	early inc. v late inc.	0.47	0.64
	late inc. v brood-guard	-14.37	<0.001
	early inc. v brood-guard	-12.05	<0.001
Black-browed albatross	early inc. v late inc.	-5.16	<0.001
	late inc. v brood-guard	-19.90	<0.001
	early inc. v brood-guard	-15.80	<0.001
Grey-headed abatross	early inc. v late inc.	-8.00	<0.001
	late inc. v brood-guard	-20.39	<0.001
	early inc. v brood-guard	-11.72	<0.001
Light mantled sooty albatross	late inc v brood-guard	-14.50	<0.001

The inter-annual variation is clearly illustrated in Figure 6.1 – 6.4 and was more pronounced during incubation than in the brood-guard stage for all species. Wandering albatrosses were the only species that showed no evidence of significant differences in incubation and brood-guard shift lengths between years (Table 6.4). The other three species all showed significant differences in mean annual incubation shift lengths (Table 6.4).

Figure 6.1
Mean shift length of Wandering albatrosses at different stages of the breeding cycle (1996/97 - 2000/01)

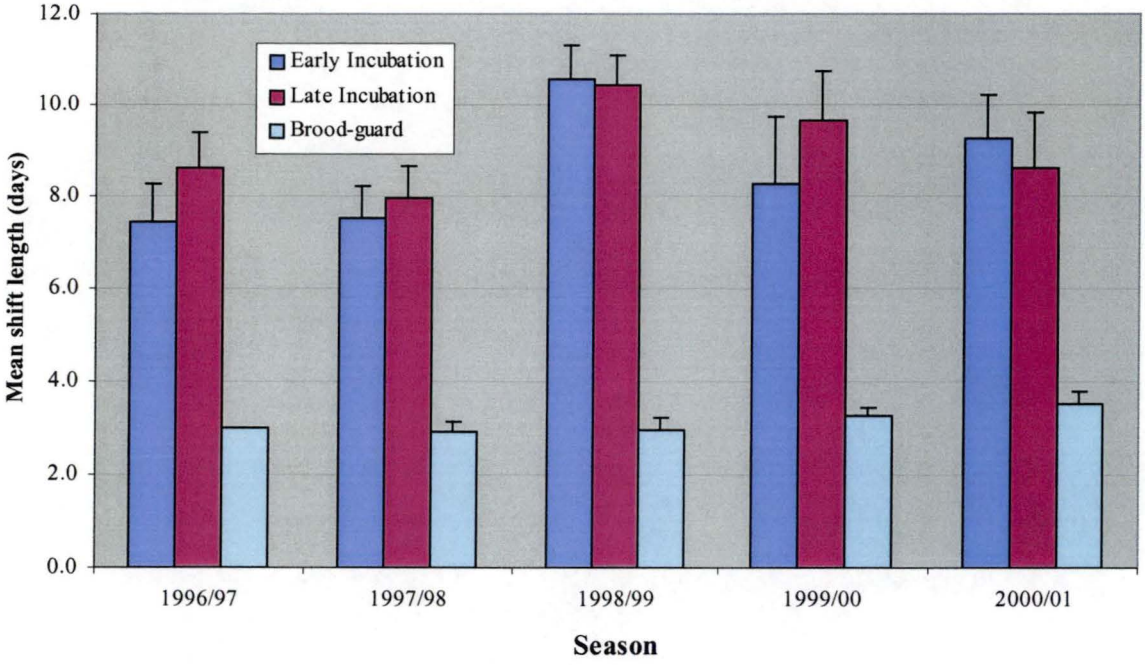


Figure 6.2
Mean shift length of Black-browed albatrosses at different stages of the breeding cycle (1994/95-2000/01)

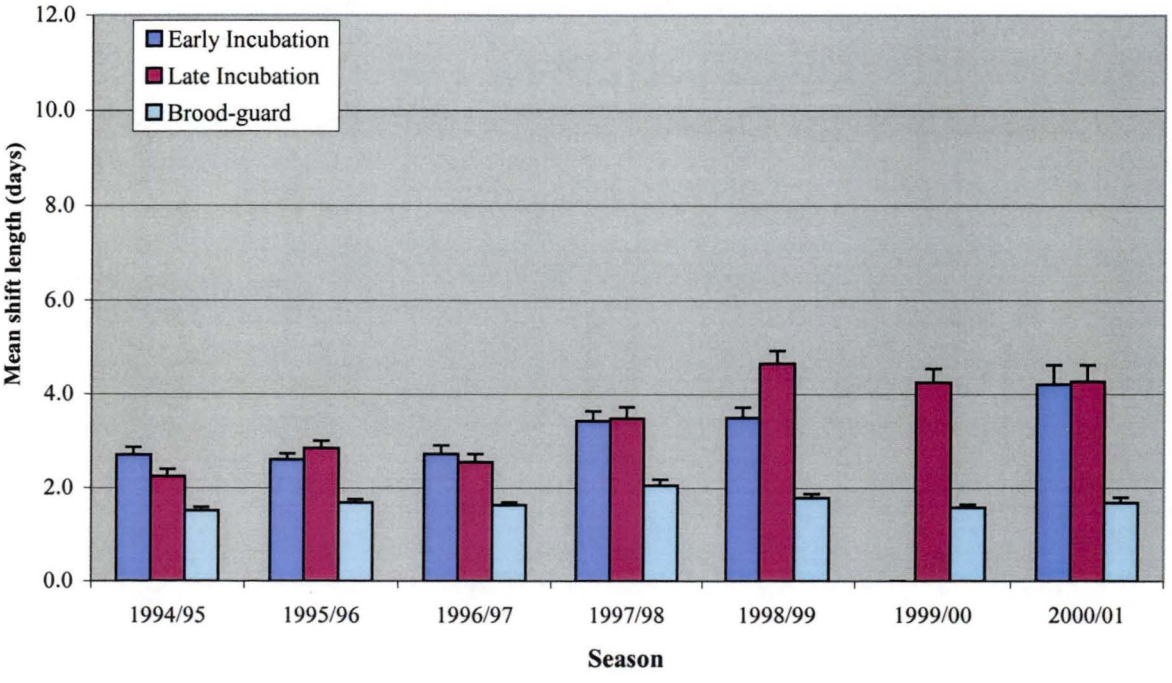


Figure 6.3
Mean shift length of Grey-headed albatrosses at different stages of the breeding cycle (1994/95 - 2000/01)

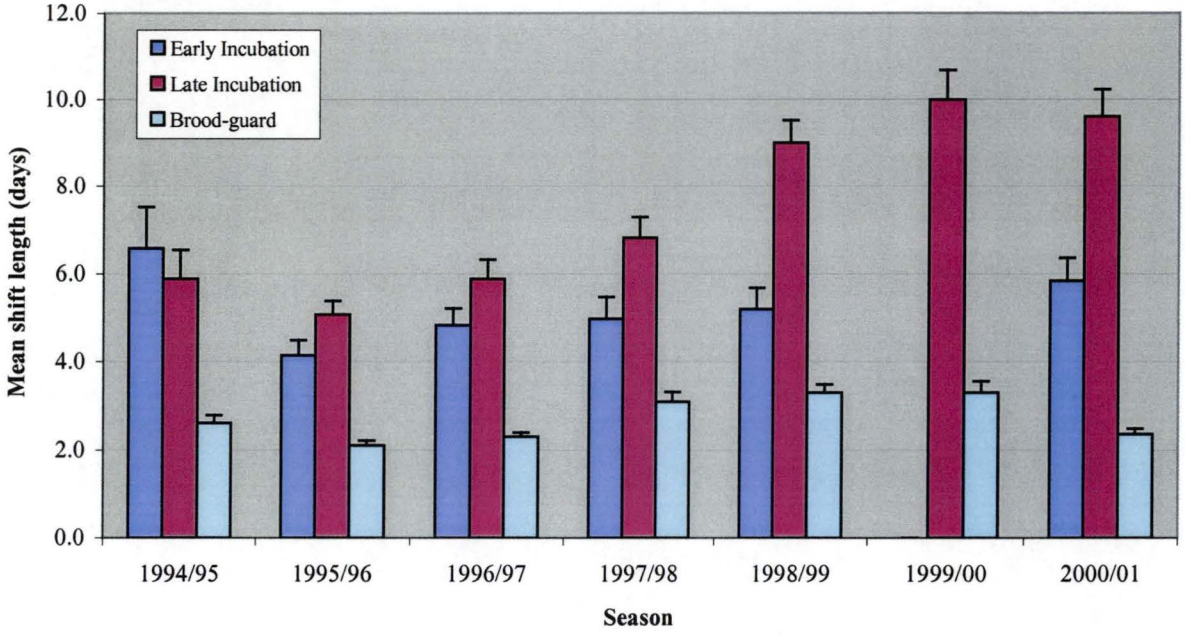
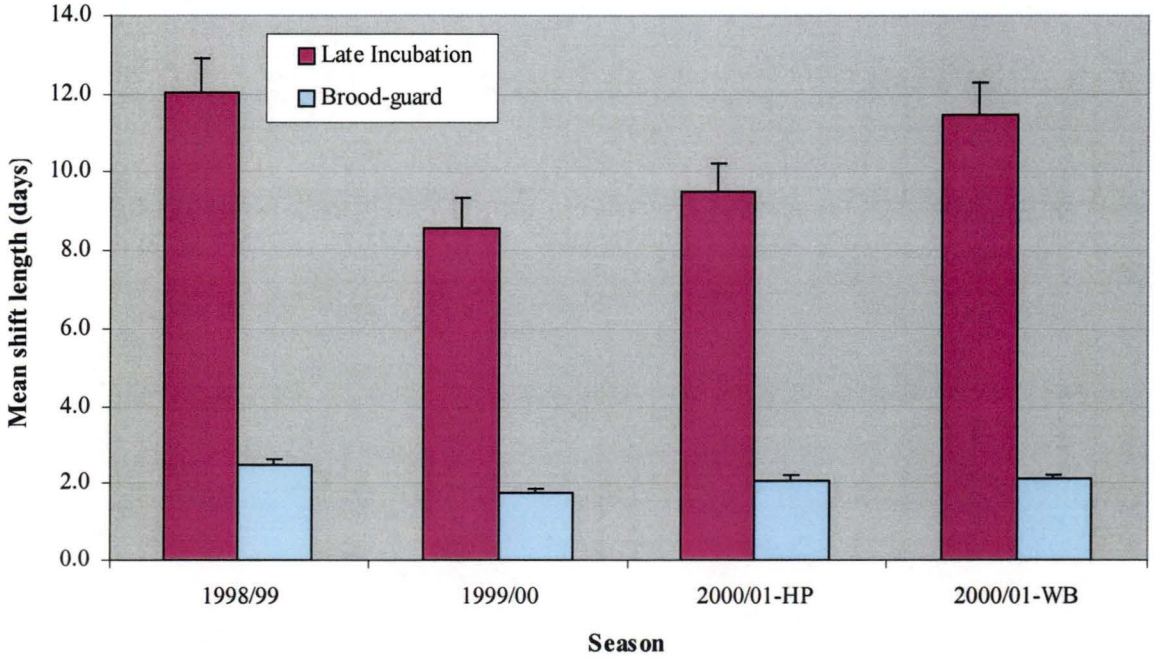


Figure 6.4
Mean shift lengths of the Light-mantled sooty albatross at different stages of the breeding cycle



These differences were most pronounced during late incubation; however, mean shift lengths of both Grey-headed and Light-mantled sooty albatrosses during the brood-guard period also varied significantly between years. Table 6.4 includes shift length data from two breeding sites during the 2000/01 season. There were no significant differences in shift length between these two sites during late incubation (Mann-Whitney U, Z=-1.59, p=0.11) or the brood-guard period (Z=-1.26, p=0.21).

Table 6.4
Summary of statistical tests (Kruskal Wallis) comparing mean shift lengths of albatrosses between years on Macquarie Island (1994/95 - 2000/01)

Species	Comparison	χ^2	df	p-value
Wandering albatross	early incubation	3.1	5	0.692
	late incubation	4.5	5	0.474
	brood guard	3.3	4	0.501
Black-browed albatross	early incubation	23.6	5	<0.001
	late incubation	58.1	6	<0.001
	brood guard	10.4	6	0.110
Grey-headed abatross	early incubation	11.2	5	0.048
	late incubation	67.6	6	<0.001
	brood guard	65.6	6	<0.001
Light-mantled sooty albatross	late incubation	8.1	2	0.018
	brood-guard	11.0	2	0.004

6.3.2 Male-female attendance during incubation and the brood guard stage.

The sex of all Wandering albatross breeders and most Black-browed albatross breeders was known and sex-specific differences in attendance of these species were examined. Black-browed albatrosses were sexed by observing copulation or by morphological differences (Chapter 2, Section 2.2.1.3). Wandering albatrosses could also be clearly identified by plumage differences with males noticeably whiter around the head and neck than females (Chapter 2, Section 2.2.4.2). Summary data on sex-specific attendance patterns for these two species are presented in Table 6.5 and in both cases males were observed to spend more time on the nest than females. This was true during both incubation and the brood-guard stage;

however, statistically significant differences (paired t-test) were only found during incubation (Table 6.5).

Table 6.5
Proportion of time spent on nest by male and female Black-browed and Wandering albatrosses (1994/95 - 2000/01) and results of paired t-tests for significant differences

Species	Stage	Time on nest (%)			Paired t	df	p-value
		Female	Male	s.e			
Wandering albatross	Incubation	45.8	54.1	1.3	-3.2	36	0.003
	Brood-guard	41.7	58.3	4.5	-1.8	7	0.109
Black-browed albatross	Incubation	45.0	55.0	1.9	-3.9	53	0.002
	Brood-guard	49.3	50.7	2	-0.5	30	0.63

6.3.3 Individual breeder quality and attendance patterns

The mean shift length at each stage of the breeding cycle in each season was calculated for breeders of different 'quality' (see Chapter 4) and is illustrated in Figures 6.5-6.8. In all seasons for which there were data, the mean shift length of *top* quality Black-browed albatrosses during early incubation was higher than that during late incubation. In direct contrast, the shift length of *bottom* quality Black-browed breeders during early incubation was consistently lower that that observed in late incubation. Statistical tests (Mann-Whitney U) showed that the shift lengths of *top* quality Black-browed albatrosses in early incubation were significantly higher than that observed in *bottom* quality breeders (Table 6.6).

The attendance patterns of *top* and *bottom* quality Grey-headed albatrosses were more similar although the inter-annual variation in shift lengths during the brood guard stage was higher (Figures 6.7 and 6.8). The other major discrepancy between the different quality breeders was the mean shift length during incubation in the 2000/01 season. In this season, early and late incubation shifts were very similar in the *bottom* quality breeders; however, the mean early incubation shift length of *top* breeders was twice as high relative to late incubation. However, despite these apparent trends, there were no significant differences between the pooled shift data of *top* and *bottom* quality Grey-headed breeders (Table 6.6).

Figure 6.5
Mean shift lengths of *top* quality Black-browed albatrosses throughout the breeding cycle (1994/95 - 2000/01)

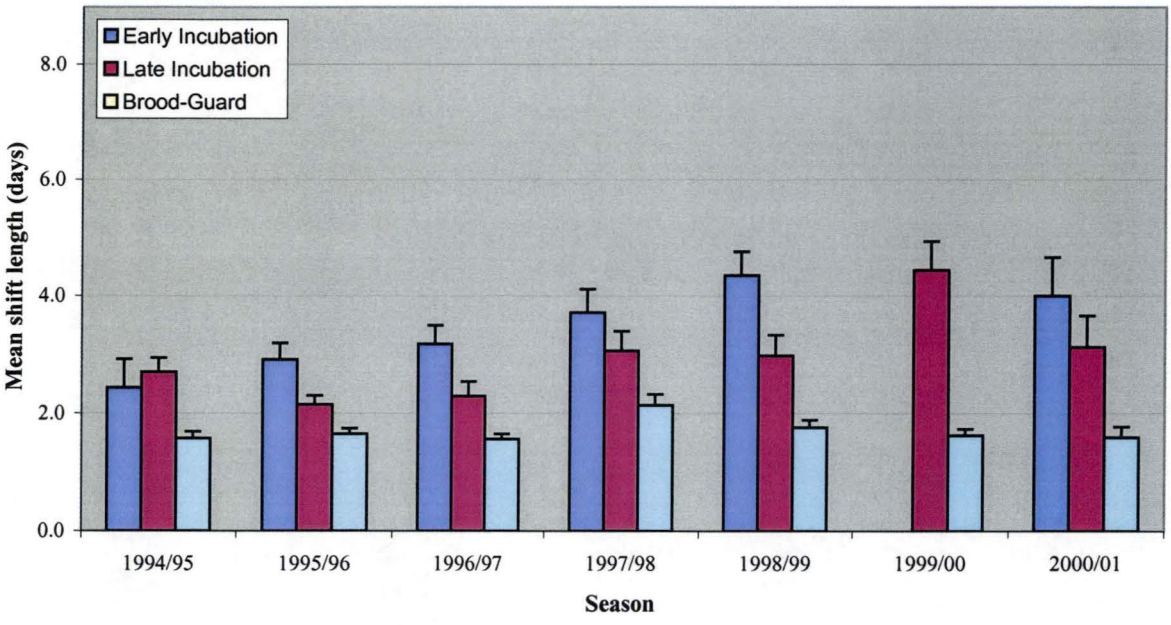


Figure 6.6
Mean shift length of *bottom* quality Black-browed albatrosses throughout the breeding cycle (1994/95 - 2000/01)

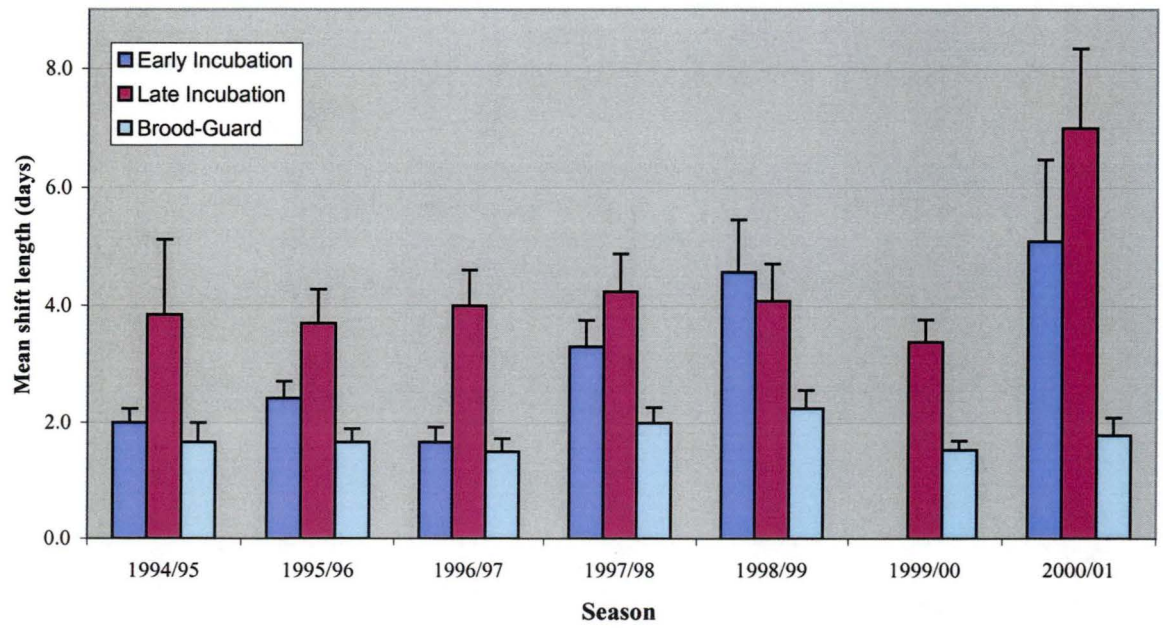


Figure 6.7
Mean shift length of *top* quality Grey-headed albatrosses throughout the breeding season(1994/95 - 2000/01)

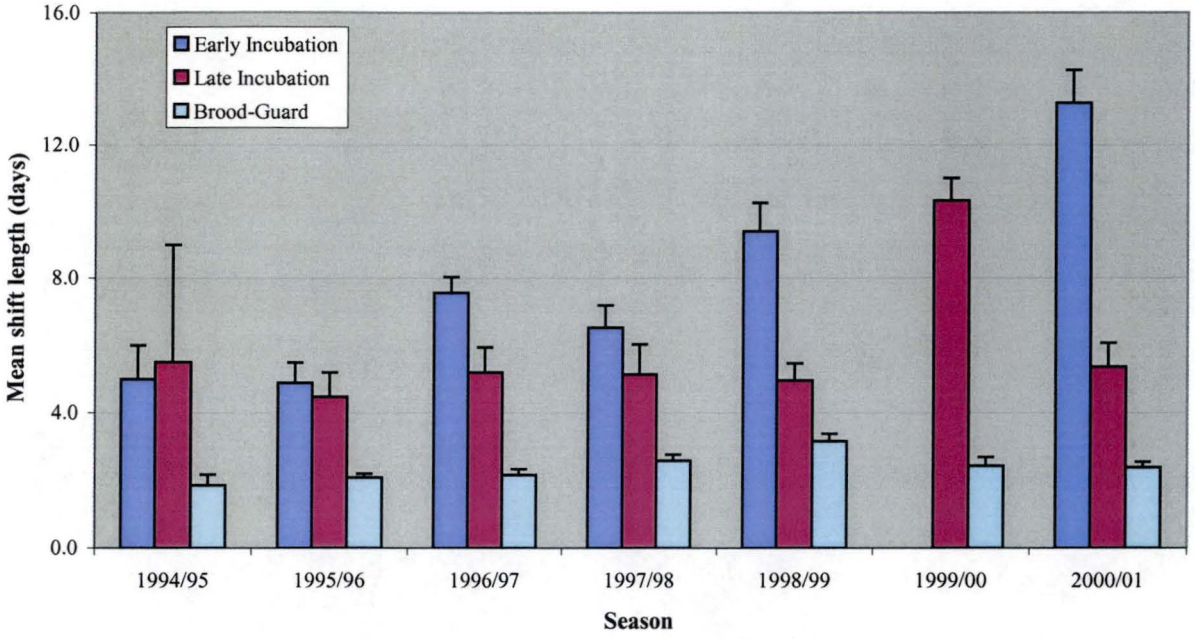


Figure 6.8
Mean shift length of *bottom* quality Grey-headed albatrosses throughout the breeding season (1994/95 - 2000/01)

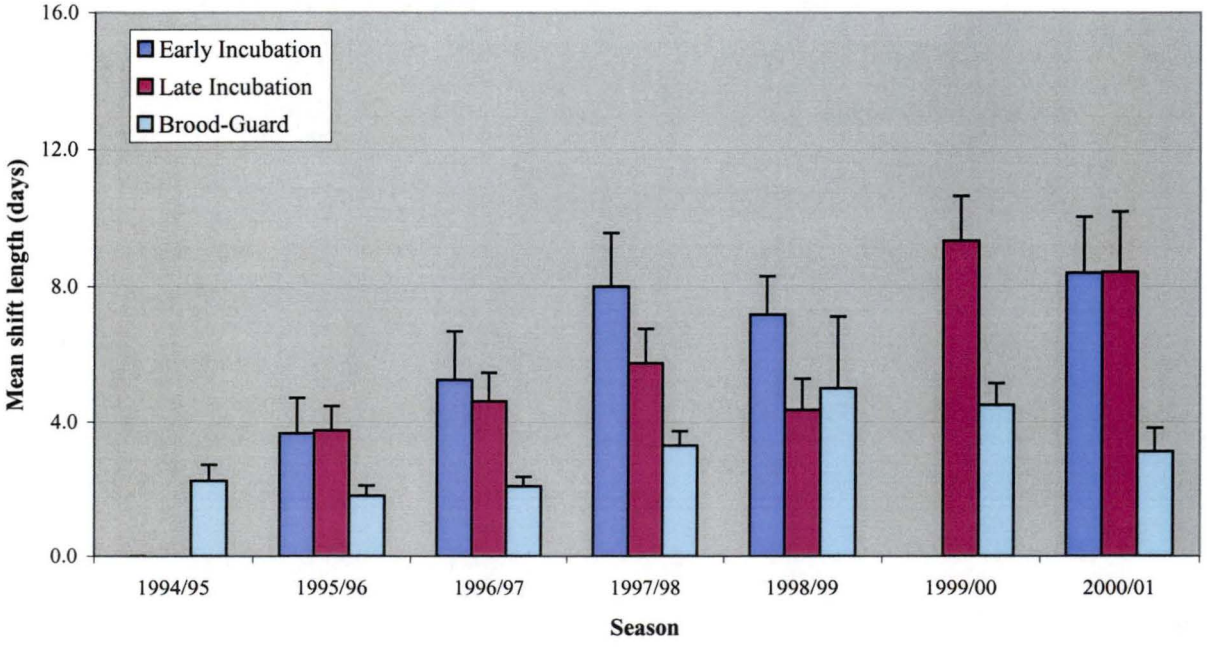


Table 6.6
Summary of statistical tests (Mann-Whitney U) comparing mean shift lengths (pooled data from 1994/95 - 2000/01) of *top* and *bottom* quality Black-browed and Grey-headed albatrosses

Species	Comparision	Z	p-value
Black-browed albatross	early inc. (*top*) v early inc (*bottom*)	-4.94	< 0.001
	late inc. (*top*) v late inc (*bottom*)	-1.83	0.067
	brood-guard (*top*) v brood-guard (*bottom*)	-0.41	0.682
Grey-headed abatross	early inc. (*top*) v early inc (*bottom*)	-0.13	0.899
	late inc. (*top*) v late inc (*bottom*)	-1.18	0.237
	brood-guard (*top*) v brood-guard (*bottom*)	-0.43	0.667

6.3.4 Attendance patterns and breeding success

Spearman Rank Correlation tests were used to test for any links between the mean shift length in each season and breeding success of Wandering, Black-browed and Grey-headed albatrosses (Table 6.7). Light-mantled sooty albatrosses were not included as there were insufficient data on shift lengths.

Four significant correlations were found. Three of these were negative and showed there was a significant relationship between mean shift length during incubation and breeding success. These correlations suggested that a longer shift length was associated with decrease in hatching success. The length of both early and late incubation shifts of Black-browed albatrosses appeared to influence hatching success while only shift length in late incubation were significantly correlated with hatching success of Grey-headed albatrosses. This is consistent with results from the analyses of the effect of individual breeder quality on attendance patterns where differences in early incubation were significant between top and bottom quality Black-browed albatrosses. No other negative correlations were observed between shift length at any other stage and breeding success; however, a positive correlation was observed between the shift length of Wandering albatrosses during late incubation and hatching success.

Table 6.7
Summary of Spearman Rank Correlation tests between mean shift length and breeding success of Wandering, Black-browed and Grey-headed albatrosses (1994/95 - 2000/01)

Species	Breeding success	early incubation			late incubation			brood-guard		
		r^s	N	p	r^s	N	p	r^s	N	p
Wandering albatross	hatch	-0.09	6	0.44	0.83	6	0.021	0.30	5	0.31
	chick	-0.27	6	0.30	0.09	6	0.43	0.67	5	0.67
	overall	-0.20	6	0.35	0.66	6	0.078	0.40	5	0.40
Black-browed albatross	hatch	-0.94	6	0.004	-0.86	7	0.007	-0.35	7	0.22
	chick	-0.31	6	0.231	-0.29	7	0.27	-0.42	7	0.18
	overall	-0.84	6	0.018	-0.64	7	0.06	-0.46	7	0.15
Grey-headed albatross	hatch	-0.14	6	0.39	-0.70	7	0.039	-0.60	7	0.08
	chick	-0.54	6	0.13	-0.34	7	0.23	-0.54	7	0.1
	overall	-0.66	6	0.078	-0.61	7	0.072	-0.67	7	0.051

positive correlation[a]
negative correlation[a]
a - 0.05 significance level adjusted (False-discovery) to account for multiple comparisons

The mean annual shift lengths of *top* and *bottom* quality Black-browed and Grey-headed albatrosses were also examined. Only three significant correlations (all related to Black-browed albatrosses) were found in these tests (Table 6.8).

Table 6.8
Significant correlations between the mean annual shift length of *top* and *bottom* Black-browed albatrosses and hatching/breeding success of the whole population

Species	Comparision (mean shift length X success)	r^s	N	p-value
Black-browed albatross	late inc. (top) **X** overall hatching success	-0.75	7	0.026
	late inc. (top) **X** overall breeding success	-0.86	7	0.007
	early inc. (bottom) **X** overall breeding success	-0.89	6	0.008

This provided further evidence that the disparity between the breeding success of *top* and *bottom* quality Black-browed albatrosses during incubation is related to shift length, which in turn is likely to be influenced by the foraging efficiency of *top* and *bottom* quality breeders.

6.4 DISCUSSION

6.4.1 Between-species comparisons

Incubation periods appeared to be size related with the smaller Light-mantled sooty albatrosses showing the shortest incubation period followed by Black-browed and Grey-headed albatrosses. Wandering albatrosses, the largest of the four species, had a significantly longer incubation period. Incubation periods were relatively consistent within each species and appear to be dictated by physiological and morphological constraints and consequently do not change in response to environmental or other external variables. The brood-guard period was more variable amongst the three smaller species ranging from 11 to 30 days. There was some evidence to suggest that the length of the brood-guard was linked to available food resources in these species; however, there were insufficient data on available food resources to quantify this relationship.

The mean shift lengths of the four albatross species breeding on Macquarie Island reflect the different foraging strategies utilised. Black-browed albatrosses had the shortest mean shift length suggesting that they generally feed closer to Macquarie Island than the other species. However, the range in individual shift length was high, particularly during incubation, where shifts as short as 0.5 days and as long as 18 days were observed. This indicates that while Black-browed albatrosses were primarily utilising resources closer to Macquarie Island, some individual breeders may have been foraging in considerably more distant waters. Satellite tracking data supported this with one Black-browed albatross foraging up to 1500 km away from the island during incubation (Chapter 7).

While the other three species did not show quite the same level of variation, a range of shift lengths were still observed during the incubation periods of the other species, indicating that breeding birds of the same species were either utilising different areas or were foraging more efficiently. The long shift lengths of Light-mantled sooty albatrosses during incubation are likely to be attributable to this species foraging at well south of the Antarctic Convergence (Weimerskirch and Robertson 1994). Similarly, the tendency of Grey-headed albatrosses to forage in pelagic waters during incubation (although not as distant as Light-mantled sooty albatrosses-Chapter 7) was also reflected by a relatively long mean shift length during incubation. Although little is known about the specific foraging areas of Wandering

albatrosses from Macquarie Island, the long mean shift lengths suggest that this species is utilising similar foraging strategies to those observed at other locations, crossing large areas of ocean in search of sporadically distributed food resources (e.g. Weimerskirch *et al.* 1993; Prince *et al.* 1998; Weimerskirch 1998).

Shift lengths of the four species during the brood-guard stage were more similar reflecting the food requirements of the young chick. In the first few weeks of life, chicks need to be supplied with food on a regular and frequent basis thus limiting the distances over which breeders can forage. The shift lengths during this time period suggest that all albatross species breeding on Macquarie Island utilise resources close to the island during this stage of the breeding cycle. Consequently, none of the species can be classified as solely 'pelagic' or 'neritic' feeders throughout their breeding cycle, a feature that has important implications to the management of fisheries and resources in waters adjacent to Macquarie Island.

6.4.2 Sex-biases in attendance patterns

There was a significant sex-bias in the amount of time that male and female Wandering and Black-browed albatrosses spent foraging during incubation. This is possibly due to sex-specific differences in foraging strategies and has been observed for both species at Bird Island, South Georgia (Tickell and Pinder 1975; Croxall and Ricketts 1983). Conversely, Weimerskirch (1995) reported no difference in the amount of time that male and female Wandering albatrosses spent incubating at Iles Crozet, perhaps reflecting less segregation of the foraging areas. Light-mantled sooty albatrosses also showed a sex-bias in the amount of time spent incubating at Iles Kerguelen with females undertaking longer shifts than males (Weimerskirch *et al.* 1986).

At Macquarie Island there were no significant differences in the time that male or female Wandering and Black-browed albatrosses spent foraging during the brood-guard stage, was consistent with observations made at Iles Kerguelen (Weimerskirch *et al.* 1986).

6.4.3 Comparisons with other locations

The breeding parameters and mean shift lengths for Wandering, Black-browed, Grey-headed and Light-mantled sooty albatrosses at Macquarie Island and other locations are summarised in Table 6.9. The mean duration of the incubation and the brood-guard stage at all locations are very similar for each species, providing further evidence that the timing of these periods is physiologically hard-wired into each species and accordingly does not show significant variation.

Table 6.9

Breeding parameters and mean shift lengths of Wandering, Black-browed browed, Grey-headed and Light-mantled sooty albatrosses and close conspecifics at five subantarctic breeding locations

Data are in days ± 1 standard deviation [A], parentheses indicate sample size

Location	Incubation period	Incubation shift		Brood-guard period	Brood-guard shifts	Age at fledging	Source
		early	late				
Wandering albatross (*Diomedea exulans*)							
Macquarie Island	79.2 ± 0.9 (32)	8.8 ± 6.0 (184)	8.8 ± 4.9 (210)	30.1 ± 3.1 (15)	3.1 ± 1.6 (229)	273.6 ± 18.6 (27)	this study
Iles Crozet	78	14.0 ± 9.0 (11) [B]	9.6 ± 4.6 (5)	31-38	2.8 ± 0.9 (15)	-	Weimerskirch *et al.* 1986; Weimerskirch *et al.* 1993, Weimerskirch 1995
Bird Island	78.4 ± 1.2 (163)	20.5 (19) [B]		32 (74)	2.6 (818)	278	Tickell 1968; Croxall and Ricketts 1983; Croxall 1991
Grey-headed albatross (*Thalassarche chrysostoma*)							
Macquarie Island	71.7 ± 1.3 (104)	5.0 ± 3.5 (321)	7.5 ± 4.0 (320)	24.8 ± 3.3 (93)	2.5 ± 1.7 (902)	128-143	this study
Bird Island	72.4 ± 1.6 (103)	11.8 ± 1.1 (41)		22.6 ± 2.8 (27)	2.9 (196)	141	Tickell and Pinder 1975; Prince *et al*. 1981; Croxall et al. 1988
Iles Crozet	73.2 ± 1.3 (18)	9.2 (132) B		23.1 ± 3.8 (15)	2.4 ±.1.1 (135)	-	Weimerskirch *et al*. 1986
Light-mantled sooty albatross (*Phoebatria palpebrata*)							
Macquarie Island	66.5 ± 1.0 (12)		10.5 ± 4.6 (122)	19.9 ± 2.2 (29)	2.1 ± 1.1 (268)	139.7 ± 6.3 (6)	this study
Marion Island	66.6 ± 1.5 (3)	21.5 ± 5.7 (4)	9.5 ± 5.4 (12)	19.5 ± 1.3 (3)	2.8 ± 1.1 (22)	170-175 (1)	Berruti 1979
South Georgia	69.9 ± 1.3 (22) [C]	12.5 ± 4.4 (17) [C]	12.0 ± 7.0 (21) [C]	20.2 ± 2.6 (6) [C]	2.7± 0.7 (45) [C]	*c.* 141	Thomas *et al.* 1983
Iles Crozet	68.7 ± 1.2 (3) [C]	9.4 ± 5.0 (9) [C]	14.3 ± 3.2 (10) [C]	-	-	*c*. 150	Mougin, 1970 (cited in Berruti 1979 and Thomas 1983)
Iles Crozet	66.9 ± 1.4 (24)	11.5 (134) [B]		19.3 ± 3.3 (13)	2.6 ±.1.6 (72)	157 ± 10.6 (43)	Weimerskirch *et al.* 1986
Black-browed albatross (*Thalassarch melanophrys*)							
Macquarie Island	68.9 ± 1.6 (103)	3.1 ± 2.6 (947)	3.6 ± 2.7 (661)	22.4 ± 4.5 (98)	1.7 ± 1.1 (1282)	110-127	this study
Bird Island	68.1 ± 1.2 (72)	13.2 ± 5.8 (33)		21.6 ± 2.8 (49)	2.5 (145)	116	Tickell and Pinder 1975; Prince *et al.* 1981; Croxall *et al*.1988
Iles Kerguelen	-	-	-	22 (25)	-	125 (54)	Weimerskirch et al. 1986

[A] - standard deviation used in this table in order to facilitate comparisons with other studies

[B] - indicates that first shift was excluded from analyses

c - indicates values were calculated from data in published papers

The only documented record of prolonged incubation was reported by Huin (1997), who recorded a Black-browed albatross incubating and successfully hatching an egg at Bird Island after 76 days.

More variation was observed in the mean shift lengths between sites. Comparisons with some studies were difficult as most averaged shift lengths over the entire incubation period. In some cases the mean shifts for early and late incubation were calculated from data presented in the published papers (e.g. Mougin 1970; Berruti 1979; Thomas *et al.* 1983). Meaningful comparisons with Macquarie Island were also confounded by the exclusion of the first incubation shift in some studies (e.g. Tickell 1968; Weimerskirch *et al.* 1986; Croxall 1991). Never-the-less, enough analogous data were obtained to compare shift lengths of all species on Macquarie Island with most locations. As with the between species comparisons, most variation was observed in incubation shift lengths and brood-guard shifts were relatively consistent at all sites.

The mean incubation shift lengths of Wandering albatrosses on Macquarie Island were considerably shorter than those observed at Iles Crozet or South Georgia (Table 6.9). This could be attributable in part to the inclusion of the first shift in the Macquarie Island calculations; however, it may also indicate that the Macquarie Island population does not generally spend as much time foraging as the other two populations. Wandering albatrosses from Macquarie Island may be travelling less distance to reach food resources, or alternatively finding higher concentrations of food resources in their foraging areas.

The mean shift length of Black-browed albatrosses was also considerably shorter on Macquarie Island relative to that found on Bird Island (Table 6.9). The foraging areas of this species from South Georgia during incubation have not been comprehensively investigated; however, during the brood-guard stage the foraging area was restricted to a relatively small area encompassing the continental shelf area of the South Georgia and South Orkney Islands (e.g. see Prince *et al.* 1998). Breeding Black-browed albatrosses from Macquarie Island and Campbell Island (*T. impavida*) occasionally forage up to 1500-2000 km away from their breeding sites (Waugh *et al.* 1999a; Waugh *et al.* 2000; Chapter 7) and if breeders from the South Georgia population are utilising this type of strategy frequently then this may account for the longer mean shift length. The estimate from South Georgia was also calculated from approximately 10% of the number of birds used in the present study and in addition the earlier study was also conducted over a considerably shorter time period (Tickell and Pinder 1975).

A similar pattern was observed with Grey-headed albatrosses, as the mean incubation shifts of the Macquarie Island population were again considerably less than Bird Island and Iles Crozet (Table 6.9). Again, little is known about the foraging areas of this species at these two locations during incubation; however it is likely that the differences relate in part to differences in sample size and methodology, and also to different foraging strategies. Mean shift lengths of Light-mantled sooty albatrosses during late incubation were most similar across all sites, perhaps reflecting similarities in foraging strategies and/or foraging areas at the different breeding sites.

6.4.4 Comparison with other albatross species

When compared with other albatross species not breeding on Macquarie Island the incubation periods and mean shift lengths are most similar to those species that share similar life history attributes, and/or foraging strategies. For example, the incubation and brood-guard period of Wandering albatrosses are most similar to the similarly sized Royal albatrosses (Richdale 1952). The short shift length of Black-browed albatrosses on Macquarie Island is most similar to Shy Albatrosses (*Thalassarche cauta*), which breeds annually and also utilises primarily neritic foraging strategies during incubation (Hedd 1999). Light-mantled sooty albatrosses showed the most similarity to their conspecific the Sooty albatross (*Phoebetria fusca*) (Berruti 1979; Thomas *et al.* 1983; Weimerskirch *et al.* 1986). The similarity in the mean shift length of species with quite different life history attributes (such as Light-mantled sooty albatrosses and Wandering albatrosses for example) suggest that foraging strategy plays a fundamental role in determining attendance patterns during incubation.

6.4.5 Attendance patterns and individual breeder quality

There were significant differences in the attendance of *top* and *bottom* quality Black-browed albatrosses during early incubation with *top* quality breeding birds showing a significantly longer mean shift length during this stage of the breeding cycle. In addition, the mean shift length of *top* quality breeders in early incubation was longer than the late incubation shift length in each year. In contrast, the opposite was observed with breeders of *bottom* quality, implying that *top* quality breeding birds spend more time foraging than those of *bottom* quality during early incubation, translating to an increased chance of fledging a chick. This extra investment by *top* quality breeders may enhance their body condition sufficiently to increase their chances of successfully getting through the latter half of incubation and chick rearing. Alternatively, *bottom* quality breeders may be attempting to undertake longer shifts during early incubation but due to weaker pair bonds, the remaining partner may abandon the egg, and thus these shifts are not recorded.

The mean shift lengths of *top* and *bottom* quality Grey-headed albatrosses during the incubation or brood guard period were more similar and no significant differences were found. Cobley (1998) found that breeders of *top* quality generally had shorter shift lengths at the start of the breeding cycle; however shift lengths were not examined at this level of detail in the current study. The pattern of inter-annual variation also appeared to be similar although there was some indication that shift lengths of *bottom* quality breeding birds were more variable between years. Brood-guard shift lengths of *bottom* quality breeding birds also appeared to be more variable and were often higher than the corresponding mean shift length of top quality breeding birds. The higher variation suggests a less regimented attendance regime amongst *bottom* quality breeders, which could be attributable to less efficient foraging. Grey-headed albatrosses appear to repeatedly target specific oceanic areas, generally related to frontal systems (Nel *et al.* 2001, Chapter 7) and it is possible that *top* breeders can locate and utilise these areas more efficiently.

6.4.6 Attendance patterns and breeding success

The mean incubation shift lengths of Black-browed and Grey-headed albatrosses each year were negatively correlated with the concurrent annual breeding success, suggesting that in seasons when birds spent more time foraging during early incubation, hatching success (and subsequently breeding success) were lower. The breeding success of both species was shown to be correlated with variation in broad scale oceanographic data (chlorophyll A and sea surface height anomalies respectively – Chapter 4) and analyses of the attendance data here suggests that shift length may be one of the contributing mechanisms in this relationship. For example, the movement or decay of eddies that are associated with the prey items of Grey-headed albatrosses may result in an increase in foraging time as birds locate appropriate areas or find food in less productive areas. Such an increase could potentially disrupt the normal attendance routine of a breeding pair resulting in nest abandonment or inadequate maintenance of body condition throughout the latter half of the breeding cycle. Due to the relatively low numbers of breeding birds in the current study this would only have to occur with a few pairs to lower overall breeding success.

Negative correlations were also found between the mean shift length during late incubation of *top* quality Black-browed albatrosses and overall breeding success. In contrast, the mean shift length during early incubation of *bottom* quality Black-browed albatrosses was negatively correlated with overall breeding success. The importance of the shift length during early incubation on breeding success was also reinforced by the observation that *top* quality

breeders had longer shift lengths than *bottom* quality breeding birds during this stage of the breeding cycle. The combination of the two correlations with breeding success (i.e. *top*-early x success, *bottom*-late x success) may be an important underlying factor in the overall correlation between mean shift length in both early and late incubation and breeding success.

The correlation between hatching success and mean shift length of Grey-headed albatrosses in the early incubation period was also significant, although not as strong as for Black-browed albatrosses. Again, this result implies that in seasons when breeders spend more time foraging, breeding success is lower. Grey-headed albatrosses are central place foragers that tend to target the same areas repeatedly (Nel *et al.* 2001, Chapter 7). There is significant variation in the frontal and eddy systems within the main foraging zones of this species from Macquarie Island (Figure 4.11, Chapter 4) and it is possible such movements result in Grey-headed albatrosses spending more time looking for the prey items associated with these systems.

There were no negative correlations between mean shift lengths of Wandering albatrosses and breeding success. This independence of breeding success from attendance patterns is probably attributable to aspects of their life history that them less susceptible to variation in environmental variables (e.g. see Croxall and Ricketts 1983; Weimerskirch 1995; Croxall *et al.* 1998). The reluctance of pair bonded birds to abandon the nest, an ability to utilise stored energy reserves, and a large potential foraging area all contribute to reduce the likelihood of this species being adversely influenced by changes in oceanic productivity. The positive correlation between the mean shift length of Wandering albatrosses in late incubation and hatching success seems anomalous in the face of results from the Black-browed and Grey – headed albatrosses. However, such a correlation could be more attributable to the age and experience of the breeders than any direct link between the two parameters. For example, Croxall *et al.* (1992) showed that age and experience of female Wandering albatrosses had some effect on egg size and consequently hatching success. These birds may be foraging in different locations, feeding more, or covering more ground than other breeders that are less likely to successfully hatch a chick.

It appears that attendance patterns and breeding success are inextricably linked, particularly in the smaller species such as the Black-browed and Grey-headed albatrosses. The decrease in breeding success that results from longer foraging trips in these species appears to be due to individuals that are unable to maintain the incubation routine during such trips. Factors such as strength of pair bond, foraging efficacy, and an ability to maintain body condition throughout the breeding cycle are likely to play an important role in these failures. A strong

argument for the close relationship between resource allocation and life history attributes was presented by Boggs (1992) and it appears that a similar relationship exists between the foraging strategies, life history attributes and breeding success of the Black-browed and Grey-headed albatrosses breeding on Macquarie Island.

Appendix 6.1

Mean shift lengths for Wandering, Black-browed, Grey-headed and Light-mantled sooty albatrosses on Macquarie Island between 1994/95 and 2000/01

Species season	early incubation			late incubation			hatch			brood/guard		
	mean	s.e	n	mean	s.e	n	mean	s.e	n	mean	s.e	n
Wandering Albatrosses												
1995/96	8.7	0.86	29	8.1	0.76	35	5.7	0.33	3	-	-	
1996/97	7.4	0.70	41	8.6	0.66	37	6.5	0.81	6	3.0	0.20	55
1997/98	7.5	0.75	35	8.0	0.67	44	6.2	1.59	5	2.9	0.26	42
1998/99	10.6	1.49	35	10.4	1.08	37	5.6	1.36	8	3.0	0.17	59
1999/00	8.3	0.93	27	9.6	1.18	25	8.2	1.64	6	3.3	0.24	50
2000/01	9.3	1.27	29	8.6	0.59	32	7.2	2.06	5	3.5	0.36	23
Mean	8.8	0.44	196	8.8	0.34	210	6.6	0.59	33	3.1	0.10	229
Black-browed albatross												
1994/95	2.7	0.17	163	2.2	0.15	45	2.6	0.29	16	1.5	0.07	147
1995/96	2.6	0.13	193	2.8	0.15	99	2.7	0.43	22	1.7	0.07	308
1996/97	2.7	0.18	184	2.5	0.18	101	3.1	0.50	18	1.6	0.06	278
1997/98	3.4	0.21	161	3.5	0.24	76	2.6	0.38	16	2.1	0.13	133
1998/99	3.5	0.22	163	4.7	0.27	116	4.3	0.80	18	1.8	0.09	152
1999/00	-	-	-	4.2	0.30	137	4.2	0.91	16	1.6	0.07	183
2000/01	4.2	0.42	83	4.3	0.35	86	7.3	1.65	4	1.7	0.11	82
Mean	3.1	0.08	947	3.6	2.70	660	3.4	0.25	110	1.7	0.03	1283
Grey-headed albatross												
1994/95	6.6	0.94	24	5.9	0.65	9	5.3	0.36	17	2.6	0.19	44
1995/96	4.1	0.35	77	5.1	0.31	62	4.2	0.41	25	2.1	0.11	207
1996/97	4.8	0.37	78	5.9	0.44	53	6.0	0.56	23	2.3	0.09	236
1997/98	5.0	0.49	45	6.8	0.47	47	6.9	1.20	15	3.1	0.22	100
1998/99	5.2	0.47	49	9.0	0.52	58	4.9	0.46	16	3.3	0.18	110
1999/00	-	-		10.0	0.68	41	7.7	1.41	10	3.3	0.26	58
2000/01	5.8	0.52	48	9.6	0.63	50	6.7	0.61	6	2.4	0.12	147
Mean	5.0	0.19	321	7.5	0.22	320	5.6	0.28	112	2.5	0.06	902
Light-mantled sooty albatross												
1998/99				12.1	0.85	24	6.2	0.62	10	2.5	0.16	70
1999/00				8.6	0.78	26	5.8	1.81	4	1.7	0.12	59
2000/01-Hurd Point				9.5	0.74	32	5.4	1.03	5	2.1	0.17	62
2000/01-Windsor Bay				11.5	0.83	41	7.2	0.79	9	2.1	0.11	77
Mean				10.5	0.4	122	6.3	0.4498	28	2.1	0.07	268

Chapter 7 - Foraging areas of Black-browed and Grey-headed albatrosses during the breeding season and exploitation of mesoscale oceanographic features

7.1 INTRODUCTION

7.1.1. Satellite telemetry

Albatrosses often range over vast distances while foraging (Warham 1990) and prior to the advent of appropriately sized satellite telemetry equipment, knowledge of specific foraging locations was obtained primarily through the recoveries of banded birds (Weimerskirch *et al.* 1985; Cooper 1988; Croxall and Prince 1990; Brothers *et al.* 1997). However, only 81 recoveries from 20 000 Wandering albatrosses banded at South Georgia were recorded between 1956 and 1986 (Croxall and Prince 1990) and while useful, this methodology was not that effective at ascertaining the foraging areas of individual birds.

At sea observations are also an effective way of determining the oceanic distribution of a species (e.g. Stahl *et al.* 1985; Silverman and Nevitt 1995); however, this methodology does not generally provide information on the provenance of the birds. Some ship-based studies have recorded the location of colour-banded birds, which augments interpretation of origin (Brothers *et al.* 1997; Croxall *et al.* 1999a); however the spatial scope of such observations is restricted due to the paucity of observers on a single vessel. Since the first Wandering albatrosses (*Diomedea exulans*) were tracked on Possession Island, Iles Crozet in 1989 (Jouventin and Weimerskirch 1990), satellite tracking studies have proven to be an extremely effective method of monitoring the foraging ecology of many species of albatrosses (Croxall 1998).

Much of the seminal work has been done on Iles Crozet and South Georgia where Wandering albatrosses have been successfully tracked since the early 1990's (Jouventin and Weimerskirch 1990; Prince *et al.* 1992; Weimerskirch 1992b; Salamolard and Weimerskirch 1993; Weimerskirch *et al.* 1993; Weimerskirch 1995; Weimerskirch *et al.* 1997b; Prince *et al.* 1998; Weimerskirch 1998). Wandering albatrosses from Marion Island have also been satellite tracked (Nel et al. 2002b), as have Gibson's albatrosses (*Diomedea gibsoni*) from the Auckland Islands (Walker *et al.* 1995). These authors have shown that data of this nature complements demographic studies and greatly assist the risk assessment of this species and quantifying their interactions with fisheries.

The advent of smaller Platform Terminal Transmitters (PTTs) has subsequently allowed the foraging ecology of many smaller species to also be investigated. Weimerskirch (1998) comprehensively described the movements of five species of albatrosses from the Kerguelen Islands (Wandering, Black-browed (*Thalassarche melanophrys*), Light-mantled sooty (*Phoebetria palpebrata*), Sooty (*P. fusca*) and Yellow nosed (*T. carteri*) albatrosses) and again, satellite telemetry data were fundamental in determining foraging strategies and areas and assessing the risk posed to each population. The movements of Black-browed and Grey-headed albatrosses from South Georgia were also described in similar detail, although only foraging trips during chick rearing were reported in this study (Prince *et al.* 1998).

In addition to the work done at Iles Crozet, Iles Kerguelen and South Georgia, many other species distributed in subantarctic and Australian waters have been tracked using satellite telemetry. The foraging ecology of Campbell (*Thalassarche impavida*) and Grey-headed albatrosses was monitored using satellite telemetry on Campbell Island (Waugh *et al.* 1999a; Waugh *et al.* 2000). Other species studied in New Zealand waters include Southern bullers albatrosses (*Thalassarche bulleri*) from the Snares and Solander Islands (Sagar and Weimerskirch 1996; Stahl and Sagar 2000a; Stahl and Sagar 2000b). Satellite telemetry studies on the foraging ecology of Grey-headed albatrosses have also been conducted on Marion Island (Nel *et al.* 2000; Nel *et al.* 2001). Satellite tracking studies in Australian waters have been conducted on Shy albatrosses (*Thalassarche cauta*) (Brothers *et al.* 1998; Hedd *et al.* 2001) and non-breeding Wandering albatrosses (*Diomedea exulans*) (Nicholls *et al.* 1992; Nicholls. *et al.* 1995; Nicholls *et al.* 1997; Nicholls *et al.* 2000, Nicholls *et al.* 2002). Five breeding Light-mantled sooty albatrosses (*Phoebetria palpebrata*) from Macquarie Island were satellite tracked by Weimerskirch and Robertson (1994).

The latter study is the only satellite tracking study that has been conducted on the albatrosses of Macquarie Island prior to the current study. Many of the above studies at other locations were initiated in response to the decline of albatross populations and the identified need to determine the foraging areas of different populations more accurately. Each year risk assessments are conducted by global committees (e.g. Incidental Mortality of Albatrosses in Longline Fisheries (IMALF) working group-part of the Commission for the Conservation of Antarctic Marine Living resources -CCAMLR) and satellite tracking data are fundamental in formalising sustainable fishery management regimes (Croxall 1998). The satellite tracking data obtained here represent the first attempts at obtaining data on the foraging areas of these two species on Macquarie Island. Due to the small and vulnerable breeding populations,

satellite tracking has been restricted to small numbers of Black-browed and Grey-headed albatrosses.

7.1.2 Oceanography of the region

Macquarie Island lies approximately 1500 km SSE of Tasmania and 1100 km SSW of New Zealand. It is an isolated island with the closest land masses being the Auckland Islands (640 km NE) and Campbell Island (700 km ENE) (Scott 1994). Macquarie Island is unique in that it is an aerial exposure of uplifted ocean crust and represents the highest point of the Macquarie Ridge complex, which extends to the north and to a slightly lesser extent the south of the island. This ridge slopes down steeply on the western side of Macquarie Island to a depth of approximately 5000 m (also known as the Macquarie Trench) approximately 20 kilometres offshore (Robinson and Scott 1999). Further to the west is relatively featureless expanse that is comprised of the Emerald Basin, and further west again, the Campbell Plateau.

Associated with this bathymetry is a dynamic region of fronts and zones that together comprise the Antarctic Circumpolar Current (ACC) (Gordon *et al.* 1977). The Subantarctic Front (SAF) passes through a deep gap in the Macquarie Ridge at approximately 53°30'S, and this front represents the boundary between the warmer, saline rich waters of the Subantarctic Zone (SAZ) and the colder waters of Polar Frontal Zone (PFZ) (Belkin 1996; Trull *et al.* 2001). The Polar Front represents the southern boundary of the Polar Frontal Zone and this front passes bends around to the south of Macquarie Island at around 57°S (Trull *et al.* 2001). Further south, closer to the Antarctic shelf, two additional circumpolar fronts have been identified, the southern ACC front (SACCF) and the 'southern boundary' (SB) of the ACC (Orsi *et al.* 1995). As the movement of distinct water masses delineates these fronts and zones, they are strongly associated with different temperature regimes and have also been associated with more localised eddy and current systems (Perissinotto and Duncombe Rae 1990; Moore *et al.* 1999; Trull *et al.* 2001). Consequently they are fundamental to the distribution of primary production in the southern ocean (Piontkovski *et al.* 1995; Pakhomov and Froneman 2000; Whitehouse *et al.* 2000; Hunt *et al.* 2001) and have been shown to be directly related to the distribution of seabirds (Abrams and Lutjeharms 1986; Waugh *et al.* 1999a; Nel *et al.* 2001, Pakhomov and McQuaid 1996; Weimerskirch and Cherel 1998).

In an attempt to clarify the mechanisms underlying the choice of foraging areas utilised by Black-browed and Grey-headed albatrosses breeding on Macquarie Island, the physical oceanography surrounding Macquarie Island, including the main foraging areas of these two species, was also examined. Oceanographic data utilised in these analyses included

bathymetry, the location of fronts and zones, primary productivity (chlorophyll A), sea surface temperatures and sea surface height anomalies (representing localised current and eddy systems (Park and Gamberoni 1995). This set of oceanographic parameters provided a relatively comprehensive picture of the marine environment in which these species were foraging and allowed a more comprehensive assessment of the factors influencing the foraging distribution of Black-browed and Grey-headed albatrosses.

7.1.3 Summary of research questions

1. What are the main foraging areas of Black-browed and Grey-headed albatrosses from Macquarie Island and how do they partition their resources ?

2. Are these foraging areas linked to oceanographic features such as bathymetry, frontal zones, primary productivity or sea-surface temperature ?

3. How much overlap is there between these foraging areas and fisheries ?

7.2 DATA PROCESSING AND ANALYSES

The technical details of the satellite transmitters used, the deployment methodology and a brief summary of the bird deployment details are provided in Chapter 2, Section 2.2.5.

7.2.1 Satellite data

Data were obtained from ARGOS (http://www.cls.fr/manuel/) in .dat and .diag formats. The .dat data were filtered through software (Interactive Data Language - D. Watts- Antarctic Division, Hobart and M. Sumner, Antarctic Wildlife Research Unit, University of Tasmania) that filtered out all locations that would have required speeds in excess of 90 km hr^{-1}. This is higher than maximum flying speeds calculated using the methodology of Pennycuick (1982) or suggested by Bevan *et al.* (1995), but similar to the maximum flying speed of Light-mantled sooty albatrosses estimated by Weimerskirch and Robertson (1994). This speed was used in the current study as good location hits (Location Class 1, 2 or 3), indicated that these speeds were definitely occurring on some of the commuting flights of these albatrosses. In fact, some location class data indicated that birds might have been travelling even faster on some commuting flights (in excess of 100 km hr^{-1}); however, these were not used in order to minimise potentially spurious locations. The resultant data were in seven location classes, according to the number of messages received from the satellite. The accuracy of these location classes are described in Table 7.1:

In a recent review of the accuracy of ARGOS location classes, Vincent *et al.* 2002 showed that A class hits were nearly as accurate as class 1 hits and B class hits still provided useful information. These authors also showed that A and B class hits in particular provided useful information in studies where a high degree of spatial accuracy was not required.

Table 7.1
Accuracy of ARGOS location classes [A]

Location Class	Accuracy
3	< 150 m
2	150 m accuracy < 350 m
1	350 m accuracy < 1000 m
0	> 1000 m
A	no estimate of accuracy of location
B	no estimate of accuracy of location

[A] - sourced from http://www.cls.fr/manuel

All classes were utilised in the subsequent analyses and processed using ArcInfo 8.1 (ESRI, Redlands, CA) and ArcView GIS 3.2a (ESRI, Redlands, CA) (http://www.esri.com/). Distances were measured on un-projected maps and both location of individual hits and time-spent grids were used to determine the main foraging areas of both species.

7.2.2 Oceanographic Data

Oceanographic data in the form of chlorophyll A levels, sea-surface temperature and sea-surface height anomalies were downloaded and converted to ArcView 3.2a compatible files as described in Section 4.2.2. The Australian Antarctic Division, Hobart, supplied bathymetry and frontal zone data.

The foraging areas of the two species were examined in conjunction with the above data and any relationships between them were qualitatively identified.

7.3 RESULTS

7.3.1 Location class summary

The number of hits in each location class were summarised for Black-browed and Grey-headed albatrosses in each tracking season. Only location hits obtained during foraging were

used to calculate the proportion excluded by filtering (Appendix 7.1) and the number of hits in each location class (Appendix 7.2).

7.3.1.1 Location hits excluded by filtering process

Similar proportions of location classes (LC) were excluded from both Black-browed and Grey-headed albatrosses and there was no significant difference between the two species (Appendix 7.1, paired-$t_4 = 1.2$, $p = 0.304$). The filtering process removed approximately 40% of all hits and the majority of these were LC A and LC B hits. No hits in LC 3 or LC 2 were excluded from the analysis by the filtering process.

7.3.1.2 Number of hits in each location class

Black-browed and Grey-headed albatrosses showed similar numbers and proportions of hits in each location class (Appendix 7.2). Overall Black-browed albatrosses showed a smaller proportion of LC B hits and higher LC 0 hits than Grey-headed albatrosses; however; this difference was not significant (paired-$t_4 = 0.00$, $p = 1$). Over 50% of hits used in the analyses were from LC 0 and hits from LC's A and B comprised the majority of the remainder (both species). Approximately 10 % of hits were from location class 1 and hits from LC's 2 and 3 made up less than 2% of the filtered data.

7.3.2 Deployment details, foraging trip distances and duration

All tracked albatrosses were banded; three were banded as chicks and of known age while the other five were banded as breeding adults and a minimum age was known for these birds. Five of the tracked birds were females, two were males and the sex of one Grey-headed albatross was unknown. The sex of the birds was determined by observing copulation, morphometric differences or egg laying (Chapter 2, Sections 2.2.1.3 and 2.2.2.3). Table 7.2 contains all details of the tracked birds and their foraging trips. A comprehensive description of each tracked foraging trip is contained in Appendix 7.3.

Table 7.2
Sex and age of tracked birds, deployment times and summary of foraging data obtained from satellite tracking Black-browed and Grey-headed alabtrosses between 20/12/1999 and 20/1/2000 (1999/00 season) and 28/11/2000 and 28/12/2000 (2000/01 season)

PTT_ID	Sex	Age	PTT deployment		Number and duration of foraging trips				Tracked foraging duration (days)
			Attached	Removed	Incubation		Brood-guard		
					Number	Mean (days)	Number	Mean (days)	
Black-browed albatross									
20876_99	female	12+	20/12/99	20/1/00	1 long	6.6	6 short	2.0 ± 0.3	18.7
20877_00	male	13+	28/11/00	25/12/00	1 long, 1 short	4.6 ± 0.9	-	-	9.2
20875_00	female	17	28/11/00	27/12/00	2 long, 3 short	3.7 ± 0.7	-	-	18.3
Grey-headed albatross									
20875_99	female	18	20/12/99	15/1/00	-		2 long	7.4 ± 0.8	14.8
20877_99	male	22+	20/12/99	19/1/00	1 long	10.7	2 short	3.0 ± 0.7	16.6
20874_99	female	13	20/12/99	16/1/00	1 long	10.0	3 short	1.2 ± 0.3	13
20876_00	unknown	10+	28/11/00	lost 15/12/00	1 long	7.5	-	-	7.5
20874_00	female	24+	28/11/00	lost 25/12/00	1 long	9.6	1 short	1.5	11.1
				Total/mean	**12 trips**	**5.5 ± 0.5**	**14 trips**	**2.7 ± 0.4**	

Twelve foraging trips during incubation were tracked, four from Grey-headed albatrosses and eight from Black-browed albatrosses. All tracked foraging trips of Grey-headed albatrosses during incubation were 'long' trips of five or more day's duration (mean = 9.5 ± 0.7 (s.e.) days). The foraging trips of Black-browed albatrosses during incubation were more variable with four out of the eight trips of less than five days duration (mean = 4.3 ± 0.7 days). In contrast, all Black-browed foraging trips during the brood-guard were short (mean = 2.0 ± 0.3 days) while the tracked foraging trips of the Grey-headed albatrosses during the brood-guard were more variable in length (mean = 3.2 ± 1.0 days) (see Appendix 7.3 for details).

7.3.3 Foraging areas

Foraging areas of both species were identified by three main (arbitrary) foraging indices:

1. prolonged periods of non-directional movement,
2. points between which the speed dropped below 20 km hr^{-1},
3. 50 km time spent squares in which more than five hours were spent

7.3.3.1 Black-browed albatrosses

7.3.3.1a Satellite tracks and locations

The satellite tracks and location hits of the three Black-browed albatrosses tracked are shown in Appendices 7.4 – 7.6. The location hits are only linked on foraging trips that extended into pelagic waters (and defined in this case by commuting movement into waters further than 100 km from Macquarie Island). Only two pelagic trips of this nature were made by Black-browed albatrosses during the two seasons of this tracking study, one during incubation in December 1999 and the other in December 2000. The former of these trips was a 'long' trip (defined as greater than 5 days duration) where the bird headed 325 km to the north of Macquarie Island over a 12 hr period before turning around and heading 360 km to the south-west. At this point the travelling speed of the bird increased and it covered 1300 km in a southerly direction over 1.5 days, often at speeds approaching 90 km hr^{-1}. The bird then spent 2.5 days foraging south of the Southern Boundary of the Antarctic Circumpolar Current (SB-ACC) (speed generally less than 30 km hr^{-1}) before heading north to the Polar Front and then north-west back to Macquarie Island (Appendix 7.4).

The other pelagic trip undertaken by a Black-browed albatross was also tracked during incubation but was considerably shorter (approximately 2.5 days duration) and most foraging time was spent in the vicinity of the Polar Front (Appendix 7.5). All other trips by Black-

browed albatrosses appeared to be concentrated around the Macquarie Island ridge complex to the north and south of the island and were often only one or two days duration (Appendices 7.4 – 7.6).

7.3.3.1b Time- spent squares

The amount of time spent by all Black-browed albatrosses in 50 km grid squares is shown in Figure 7.1. This clearly illustrates the concentration of foraging effort around the Macquarie Island Ridge Complex. Approximately three-quarters of all foraging time of Black-browed albatrosses was spent within the Australian Economic Exclusion Zone (delineated by a 200 nautical mile circle centred on Macquarie Island). A further 9 % of foraging time was spent in the southern foraging region, which lies entirely within the Commission for the Conservation of Antarctic Marine Living resources (CCAMLR) Statistical Sub-area 88.1. A summary of time spent in the different regions around Macquarie Island is shown in Table 7.3.

Twenty kilometre time-spent squares were also constructed to examine the foraging areas of this species at a higher resolution around Macquarie Island. Identical time spent squares were also created for the Australian Licensed Commercial Fishing Vessel (ALCFV), trawling for Patagonian Toothfish (*Dissostichus eleginoides*) in the vicinity of Macquarie Island at the same time that the telemetry studies were being conducted (using vessel Monitoring System - VMS data supplied by the Australian Fisheries Management Authority-AFMA). Figures 7.2 and 7.3 illustrate the main areas where Black-browed albatrosses were foraging as well as the concurrent fishing area of the Australian Licensed Commercial Fishing Vessel (ALCFV) during the 1999/00 and 2000/01 summers. These figures show that both the ALCFV and the Black-browed albatrosses both preferentially utilised the areas above the ridge complexes to the north and south of Macquarie Island. The green bordered areas clearly show that there is significant overlap in these areas. Approximately 50% of the foraging time of the Black-browed albatross was spent in the same area as the ALCFV in 1999/00 and this figure increased to 70% in the 2000/01 summer season (See Figures 7.2 and 7.3).

7.3.3.2 Grey-headed albatrosses

7.3.3.2a Satellite tracks and locations

The pelagic foraging trips of Grey-headed albatrosses were characterised by long fast flights to the east and east south-east of Macquarie Island, followed by concentrated foraging in a relatively confined area before returning to Macquarie Island by similar routes.

Figure 7.1
Time spent by three Black-browed albatrosses in 50km grid squares from 20/12/1999 to 20/1/2000 (1999/00 season) and from 28/11/2000 to 28/12/2000 (2000/01 season). (late incubations and early brood-guard stage)

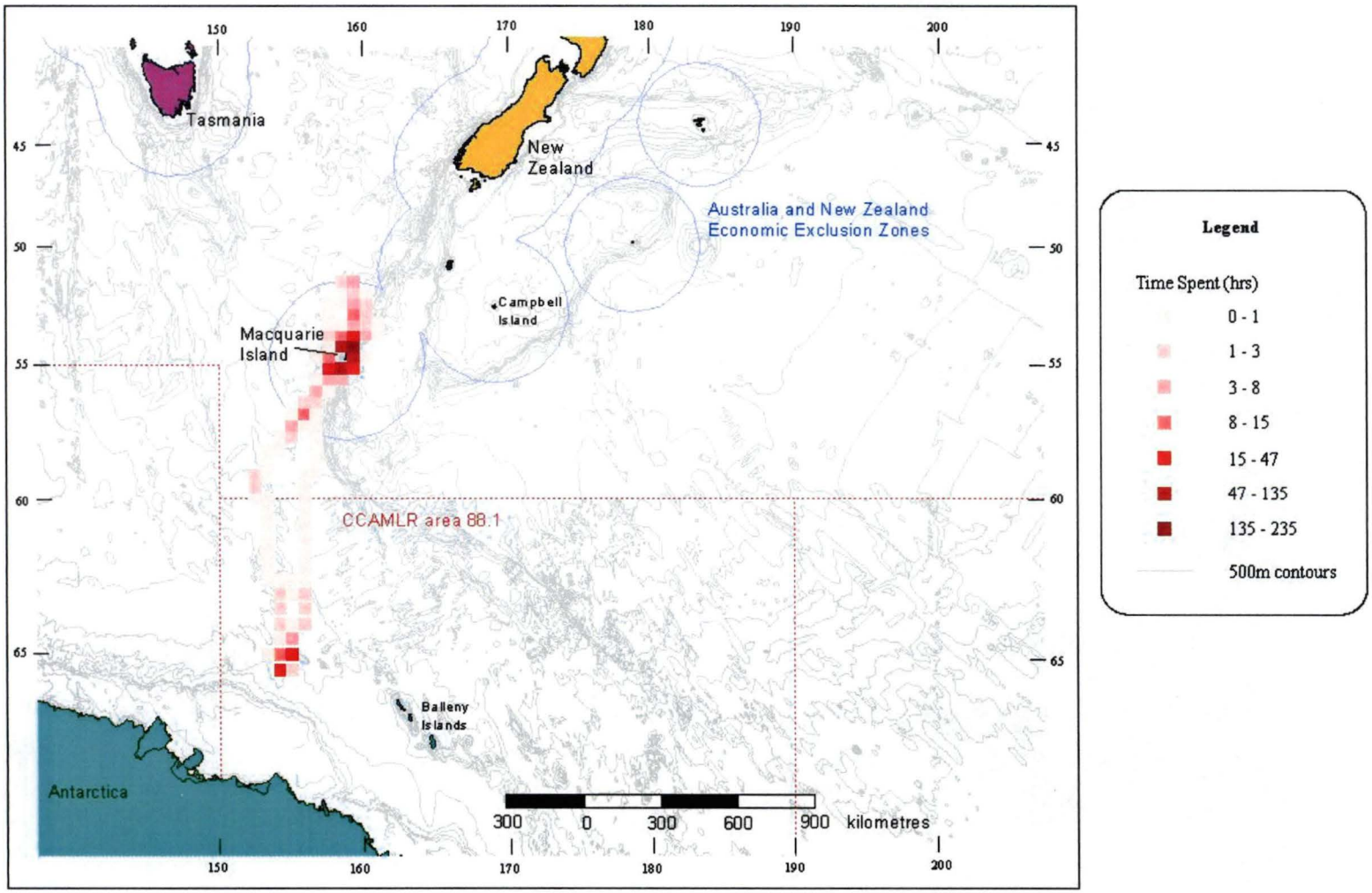


Figure 7.2
Time spent squares illustrating the areas utilised by the Australian Licensed Commercial Fishing Vessel (ALCFV) and a Black-browed albatross in December 1999 and January 2000 of the 1999/2000 season

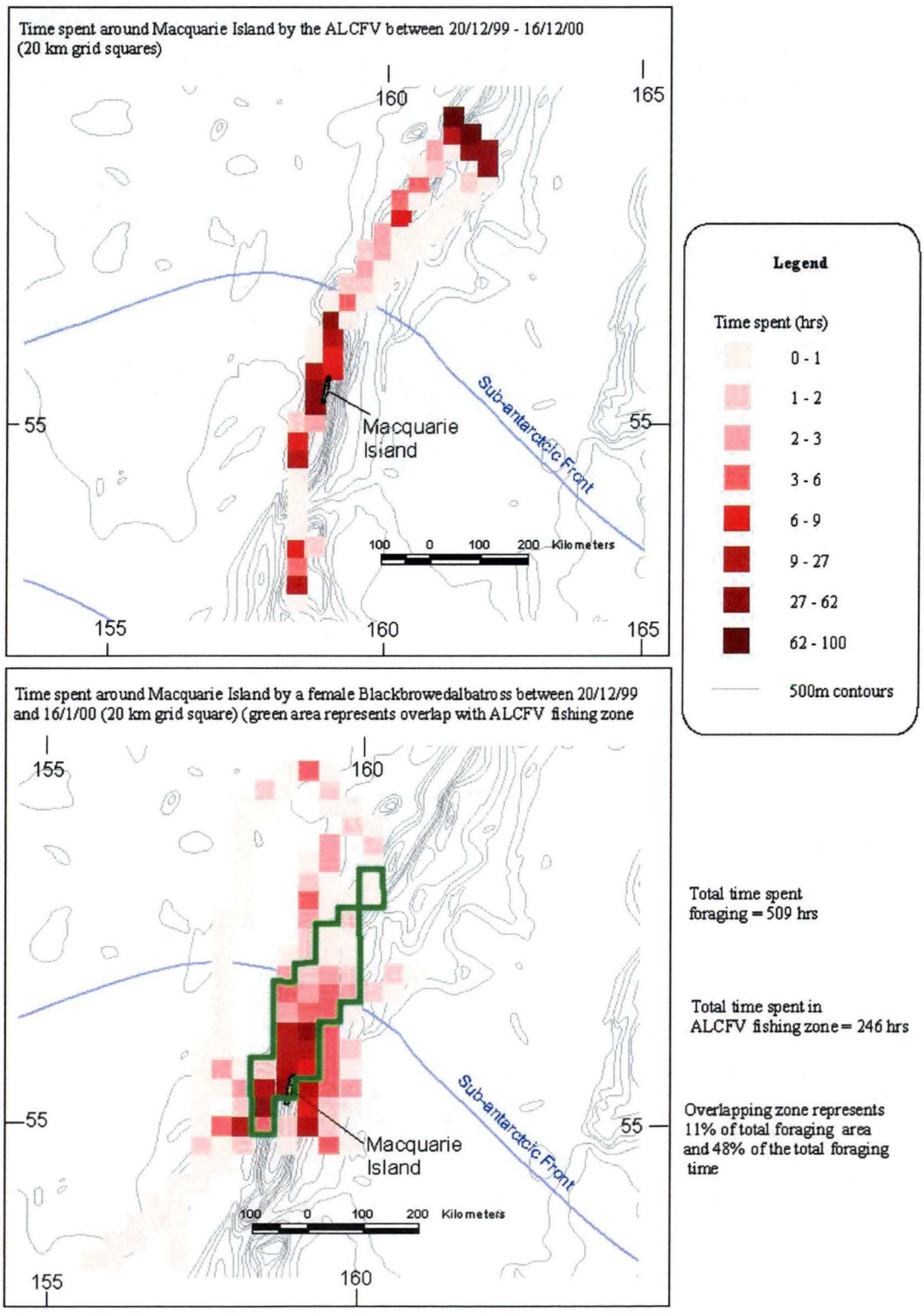
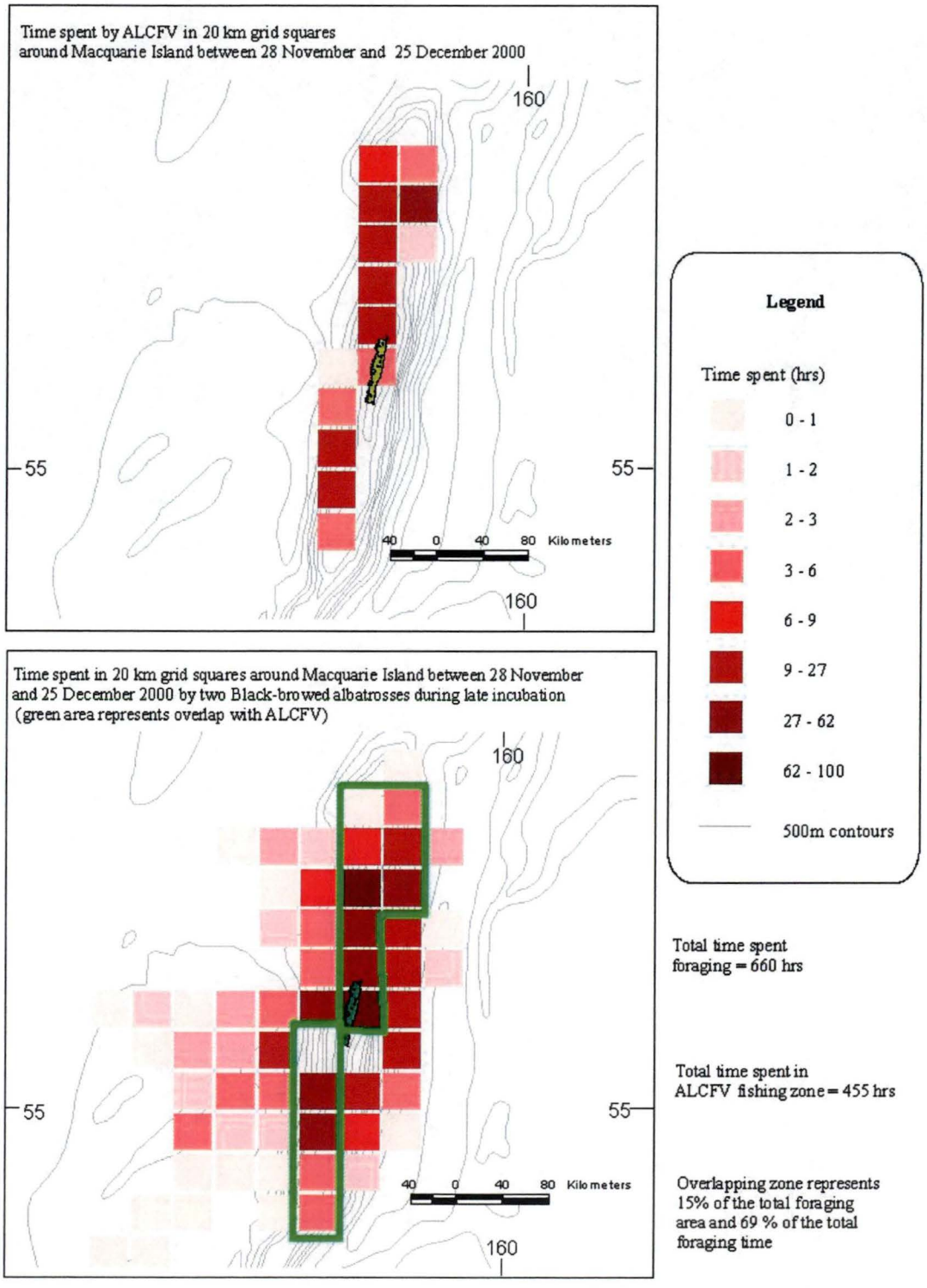


Figure 7.3
Time spent squares illustrating the areas utilised by the Australian Licensed Commercial Fishing Vessel (ALCFV) and two Black-browed albatrosses in November and December 2000



Detailed descriptions of the foraging movements are contained in Appendix 7.3 and the tracks of each Grey-headed albatross and the main foraging areas are shown in Appendices 7.7 to 7.11. Travelling speeds on the outward commuting leg were often in excess of 70 km hr^{-1} and distances of up to 2000 km were regularly covered over 24 to 48 hours. Speeds on the return leg were consistently lower, generally between 30 and 60 km hr^{-1} and characterised by short bursts of foraging activity. In a similar manner to the Black-browed albatrosses many of the directional changes of the Grey-headed albatrosses appeared to occur in the vicinity of the frontal systems, particularly the Subantarctic Front and to a lesser extent the Polar Front. Much of the foraging time appeared to be just to the north or just to the south of the Subantarctic Front or within the Polar Frontal Zone (Appendix 7.3 for descriptions and Appendices 7.7 - 7.11 for tracks).

7.3.3.2b Time spent squares

Fifty kilometre time spent squares were created from all the filtered Grey-headed albatross telemetry data (both seasons, all birds) and these are illustrated in Figure 7.4. This figure shows that Grey-headed albatrosses from Macquarie Island also foraged in the Australian and New Zealand Economic Exclusion Zone (36% of total time spent foraging) and CCAMLR Statistical sub-area 88.1 (13% of total foraging time) (Table 7.4). The remainder of the foraging time appeared to be spent primarily in two locations to the east and east south-east of Macquarie Island. Figures 7.5 and 7.6 show that these locations remained relatively consistent between the two years of the satellite telemetry study, although significantly fewer data were obtained in the 2000/01 summer due to the loss of PTTs. These latter two figures also indicate that Grey-headed albatrosses regularly foraged over the Subantarctic and Polar Fronts whilst travelling to and from their established foraging areas

7.3.3.3 Foraging areas and the Macquarie Island Marine Park

The Macquarie Island Marine Park was proclaimed under the *National Parks and Wildlife Conservation Act 1975* on 27 October 1999. The Marine Park was proclaimed to protect the "unique and vulnerable marine ecosystems of the south-east portion of the Commonwealth waters around Macquarie Island" (Environment Australia 2001b). The Marine Park covers an area of approximately 16 million hectares, and consists of a central Highly Protected Zone (IUCN category I – no commercial or recreational fishing allowed ~5.8 million hectares) lying between two Habitat/Species Management Zones (IUCN Category iv – Commercial fishing allowed with AFMA fishing concession, potential scope for other commercial ventures – ~10 million hectares) (Environment-Australia 2001).

Figure 7.4
Time spent in 50km grid squares by five Grey-headed albatrosses during the 1999/00 and 2000/01 summers on Macquarie Island

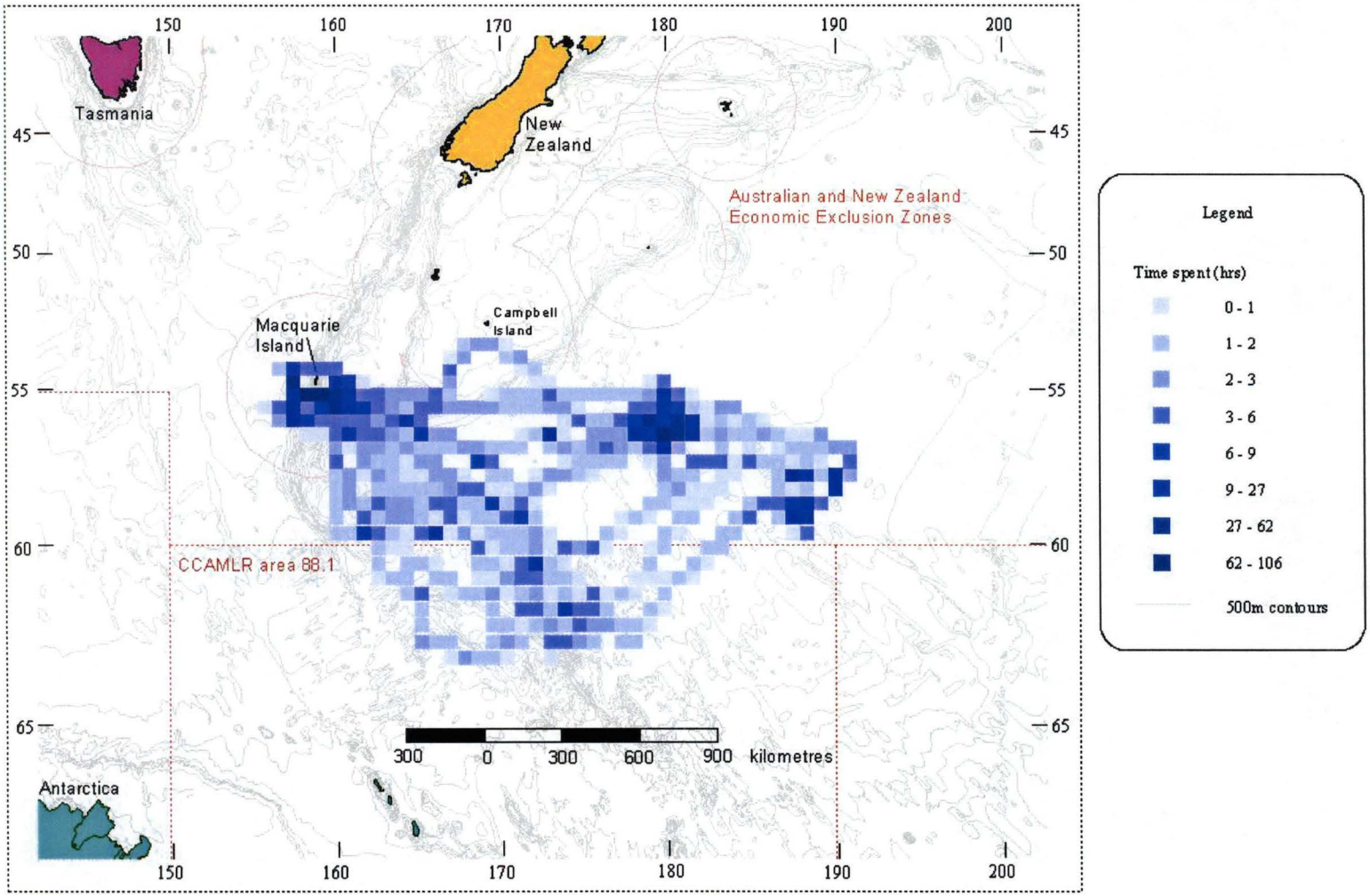


Figure 7.5
Time spent in 50 km grid square by three Grey-headed albatrosses during the 1999/00 summer on Macquarie Island

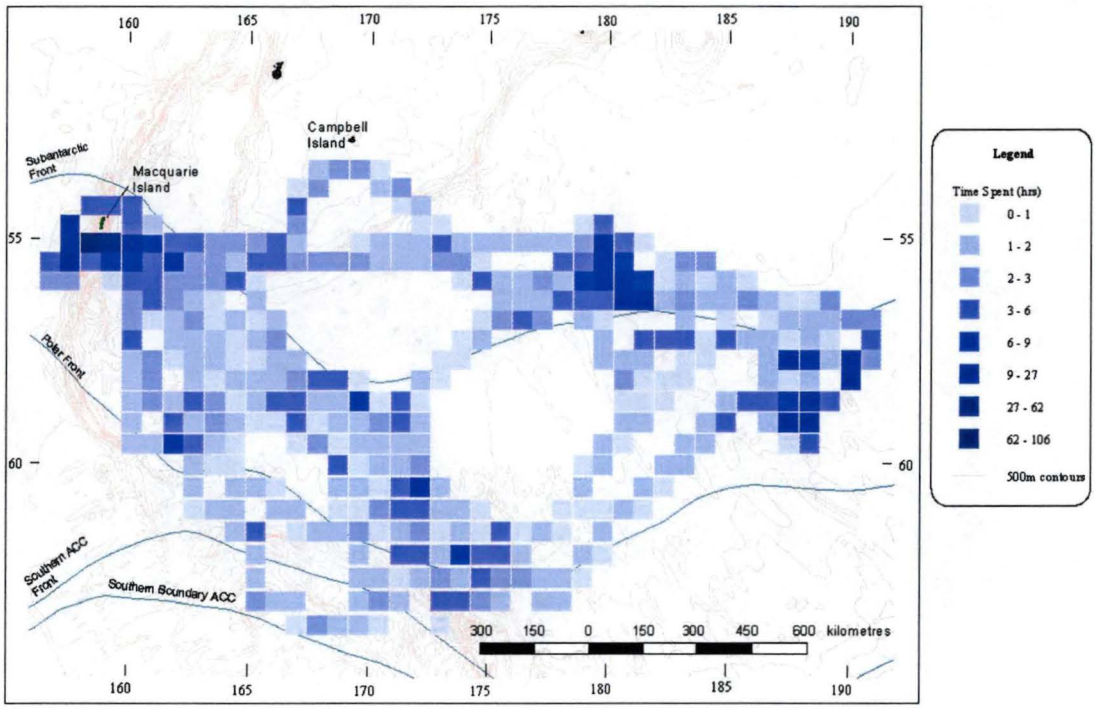


Figure 7.6
Time spent in 50 km grid squares by two Grey-headed albatrosses during the 2000/01 summer

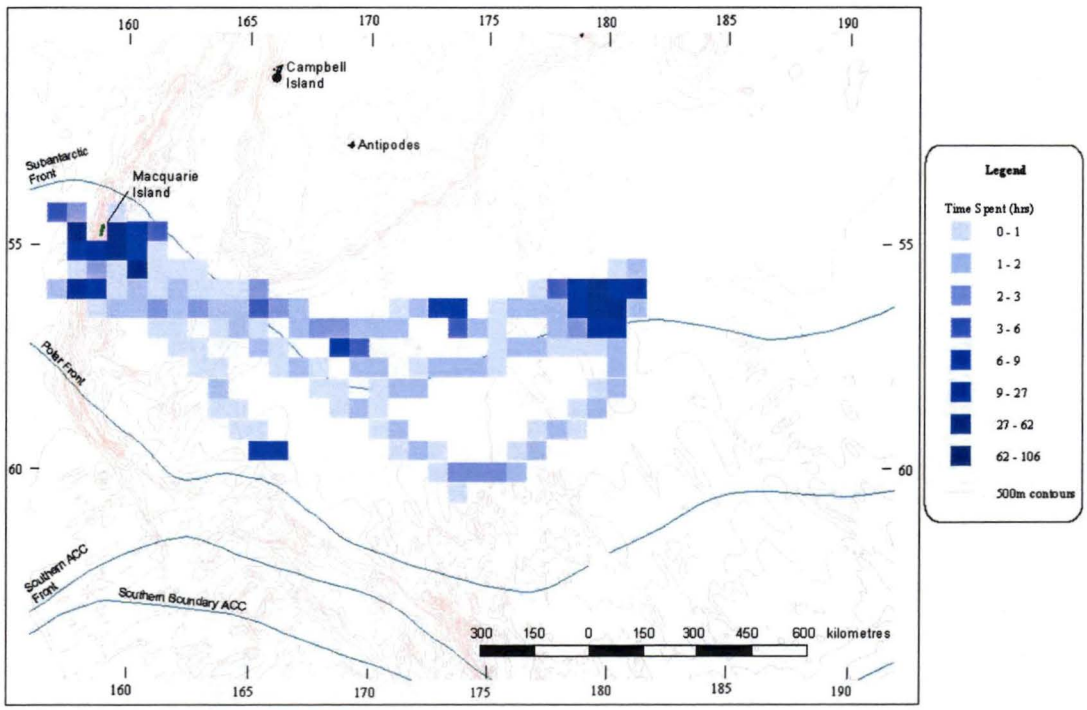


Table 7.3
Proportion of total foraging time (A) and MI EEZ foraging time spent by Black-browed and Grey-headed albatrosses in managed regions around Macquarie Island from 20/12/1999 to 20/1/2000 (1999/00 season) and from 28/11/2000 to 28/12/2000 (2000/01 season)

Species	Total tracked foraging time (days)	Percentage of total foraging time spent in different regions					
		CCA MLR 88.1	Aust. and NZ EEZ	Macq Is. EEZ	MI Marine Park	HSMZ [A]	HPZ [B]
Black-browed albatross	45	9	77	77	41	7	34
Grey-headed albatross	64	13	36	33	21	13	8

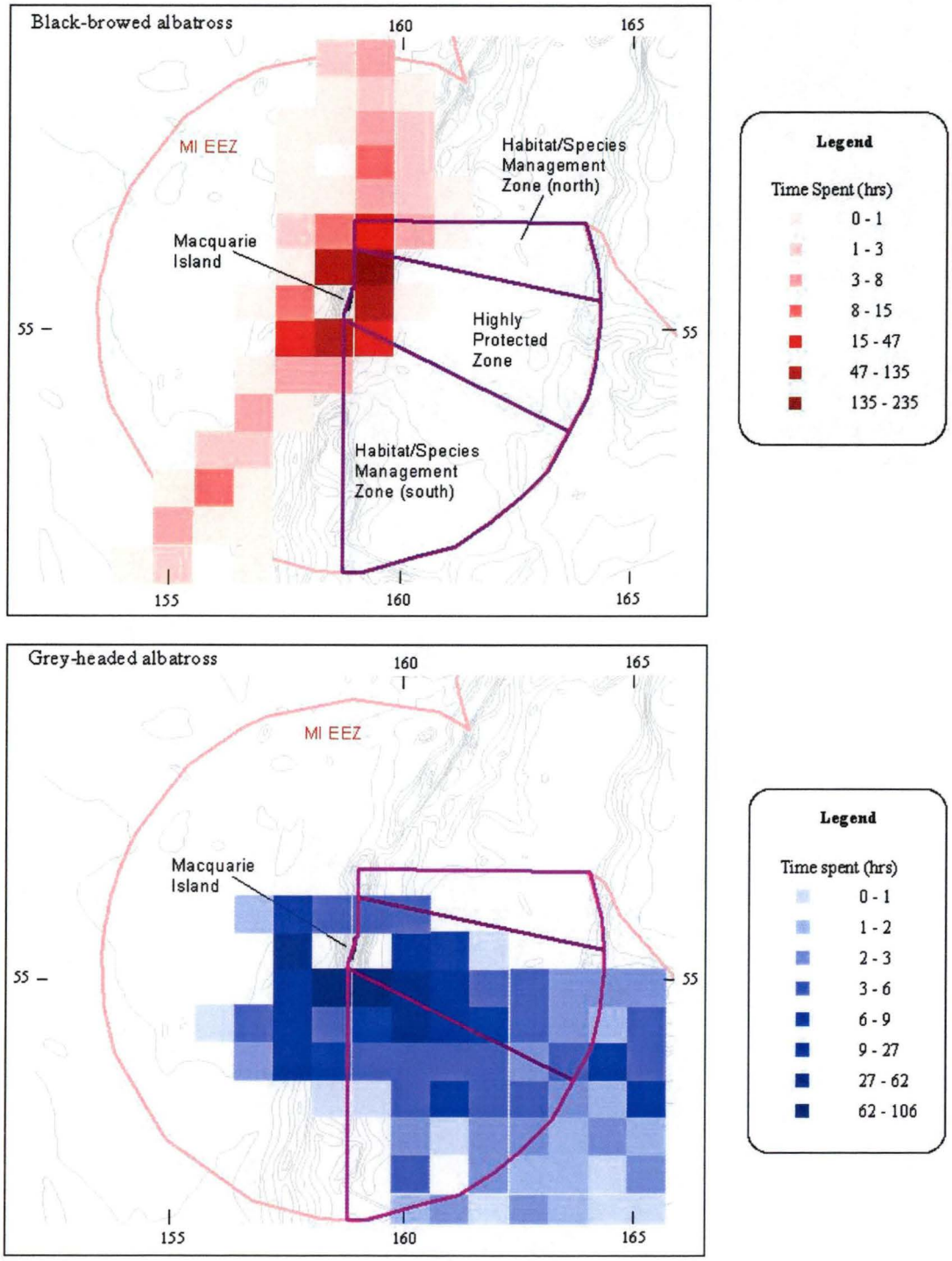
Species	Total foraging time in MI EEZ (days)	Percentage of MI EEZ foraging time spent in zones of the MI Marine Park		
		MI Marine Park	HSMZ [A]	HPZ [B]
Black-browed albatross	35	53	9	44
Grey-headed albatross	21	55	32	23

[A] - Habitat/Species Management Zones of the Macquarie Island Marine Park (Figure 7.7)

[B] - Highly Protected Zone of the Macquarie Island Marine Park (Figure 7.7)

Figure 7.7 shows the geographical area covered by the Marine Park and the corresponding time spent squares of Black-browed and Grey-headed albatrosses. Approximately 41% and 21% of the total foraging time of Black-browed and Grey-headed albatrosses respectively was spent in the Macquarie Island Marine Park (Table 7.3).

Figure 7.6
Area covered by the zones of the Macquarie Island Marine Park and the associated time spent by Black-browed and Grey-headed albatrosses in 1999/00 and 2000/01



Around three-quarters of this time was spent in the Highly Protected Area by Black-browed albatrosses; while an even smaller proportion of the foraging time of Grey-headed albatrosses was spent in this zone (Table 7.3). Examination of the data on a more localised geographic scale revealed that of the time that both species spent in the Macquarie Island EEZ less than half was spent in the Marine Park. Both species clearly spend significant amounts of time foraging in the Macquarie Island EEZ and not in the Marine Park, suggesting that the boundaries of the Marine Park may need to be reviewed in order to adequately protect the marine habitat of these species. Of the time that Grey-headed albatrosses spent foraging within the Marine Park, over one-third was spent in the Habitat/Species Management Zone, providing further impetus for a review of the Marine Park boundaries and classification of zones.

7.3.4 Oceanography and foraging areas.

In an attempt to understand the routes taken and the foraging areas utilised by Black-browed and Grey-headed albatrosses from Macquarie Island, oceanographic data were obtained and mapped in conjunction with the concurrent foraging points. Foraging points were defined as those between which the speed was less than 20 km hr^{-1}, and the centre of a 50 km grid square in which a tracked bird spent more than five hours. Frontal zones (as described by Orsi *et al.* 1995; Trull *et al.* 2001, 20 year averages) are also included on these maps of oceanographic data.

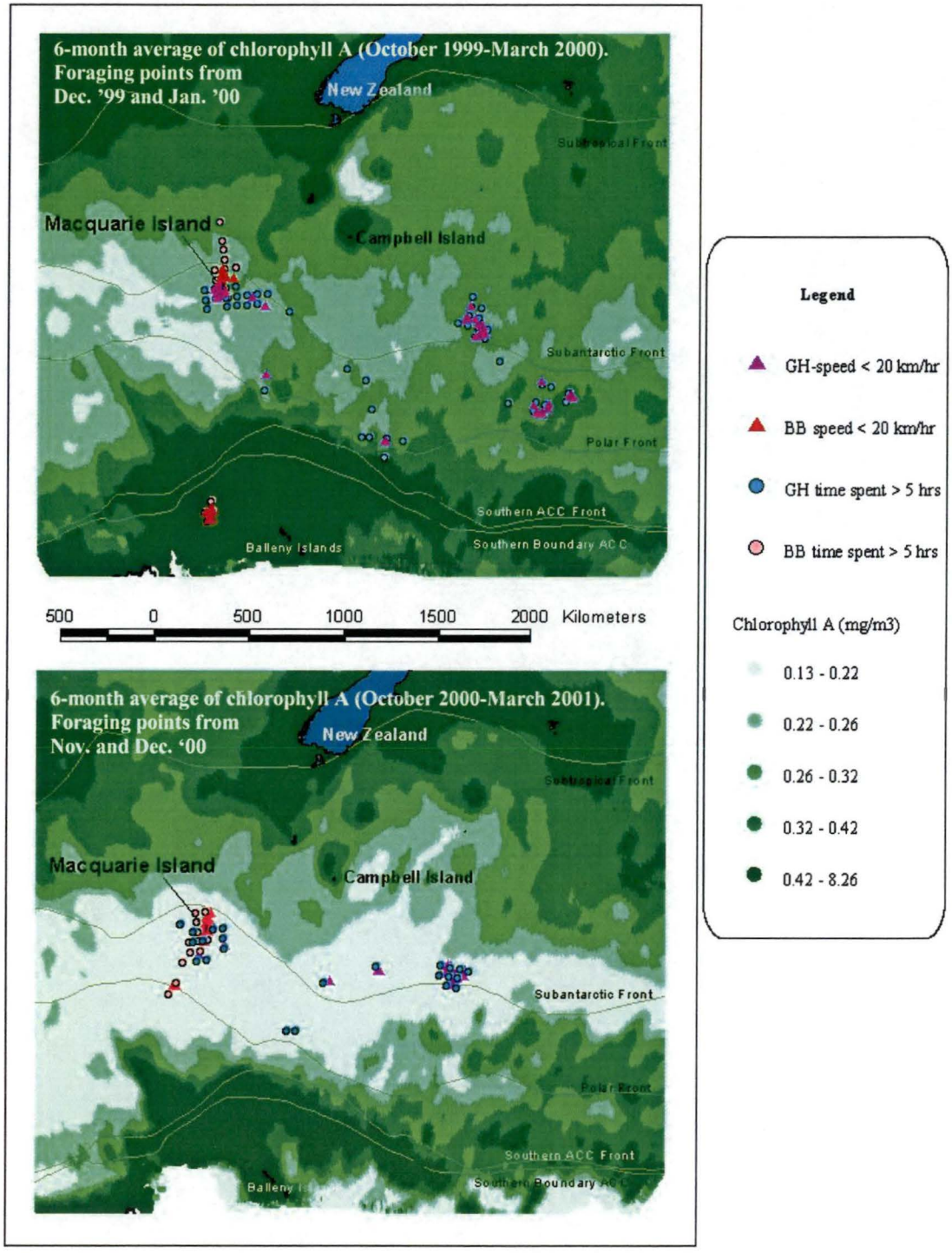
7.3.4.1 Frontal zones

The fronts to the east and lesser extent the south of Macquarie Island appeared to play an important role in directional changes made by birds travelling to and from foraging areas. Figure 7.7 shows that these zones are also important during foraging. Both Black-browed and Grey-headed albatrosses spent many days foraging in the vicinity of the Subantarctic Front. Grey-headed albatrosses concentrated their foraging effort in pelagic water to the east over this zone and Black-browed albatrosses utilised this front in more neritic waters to the north of Macquarie Island. Both species also appeared to forage over the Polar Front although to a lesser extent. The fronts illustrated in Figure 7.7 are 20 year averages (following Orsi *et al.* 1995; Trull *et al.* 2001) so their actual position in each season may be slightly different to that shown.

7.3.4.2 Chlorophyll A

The chlorophyll A maps shown in Figure 7.7 are six monthly averages from October to March inclusive of the respective years.

Figure 7.7
Foraging points of Black-browed and Grey-headed albatrosses with frontal zones and chlorophyll A levels during the summers of 1999/00 and 2000/01.



This figure shows how variable chlorophyll A levels are in the waters surrounding Macquarie Island with clear differences between summers. There does appear to be some association between Chlorophyll A levels and the frontal systems, particularly in the waters in and south of the Antarctic Circumpolar Current. The Black-browed albatross tracked in 1999/00 travelled to, and foraged in these chlorophyll rich waters and most other foraging points were concentrated around highly productive waters close to Macquarie Island. In contrast, the foraging movements of Grey-headed albatrosses appeared to be largely independent of chlorophyll levels and there was only slight evidence in 1999/00 that some of the foraging points to the east and south in 1999/00 may have been associated with high chlorophyll A levels.

7.3.4.3 Sea surface temperature

Figure 7.8 illustrates the distribution of Sea-Surface Temperature around Macquarie Island in 1999/00 and 2000/01 (October –March averages). There appears to be a strong correlation between the frontal zones and temperature gradients and the Grey-headed albatrosses appeared to preferentially feed over these gradients in pelagic waters. A similar relationship appears to be present between the foraging areas of Black-browed albatrosses but because of the concentration of these efforts in a small area around Macquarie Island, and the paucity of high resolution sea surface temperature data in this area, this relationship is difficult to quantify. Both species appeared to concentrate feeding effort in cooler waters of temperatures between one and seven degrees Centigrade, with the exception of the long foraging trip of the Black-browed albatross in 1999. It is likely that this foraging trip is associated with the ice edge of the Antarctic continent and prey items associated with it

7.3.4.4 Sea surface height anomalies

The sea-surface height anomalies around Macquarie Island and in the vicinity of the foraging areas of Black-browed and Grey-headed albatrosses are illustrated in Figures 7.9 and 7.10. Due to the nature of the satellites and their use of radar to detect these anomalies, coverage is superior to both chlorophyll A or sea surface temperature data. Consequently, six monthly averages are not necessary and smoothing half-degree data from a ten-day period leaves few gaps in the coverage (Figures 7.9 and 7.10). These figures also show how variable these anomalies are, with vastly different anomaly patterns observed in successive ten-day periods. The foraging effort data of both species were also partitioned into the same ten-day blocks to examine high resolution temporal associations with the anomalies. Only slow speed foraging points were used for this analysis, as it was not possible to partition the time-spent data.

Figure 7.8
Distribution of sea-surface temperature and foraging points of Black-browed and Grey-headed albatrosses in waters surrounding Macquarie Island during the summers of 1999/00 and 2000/1

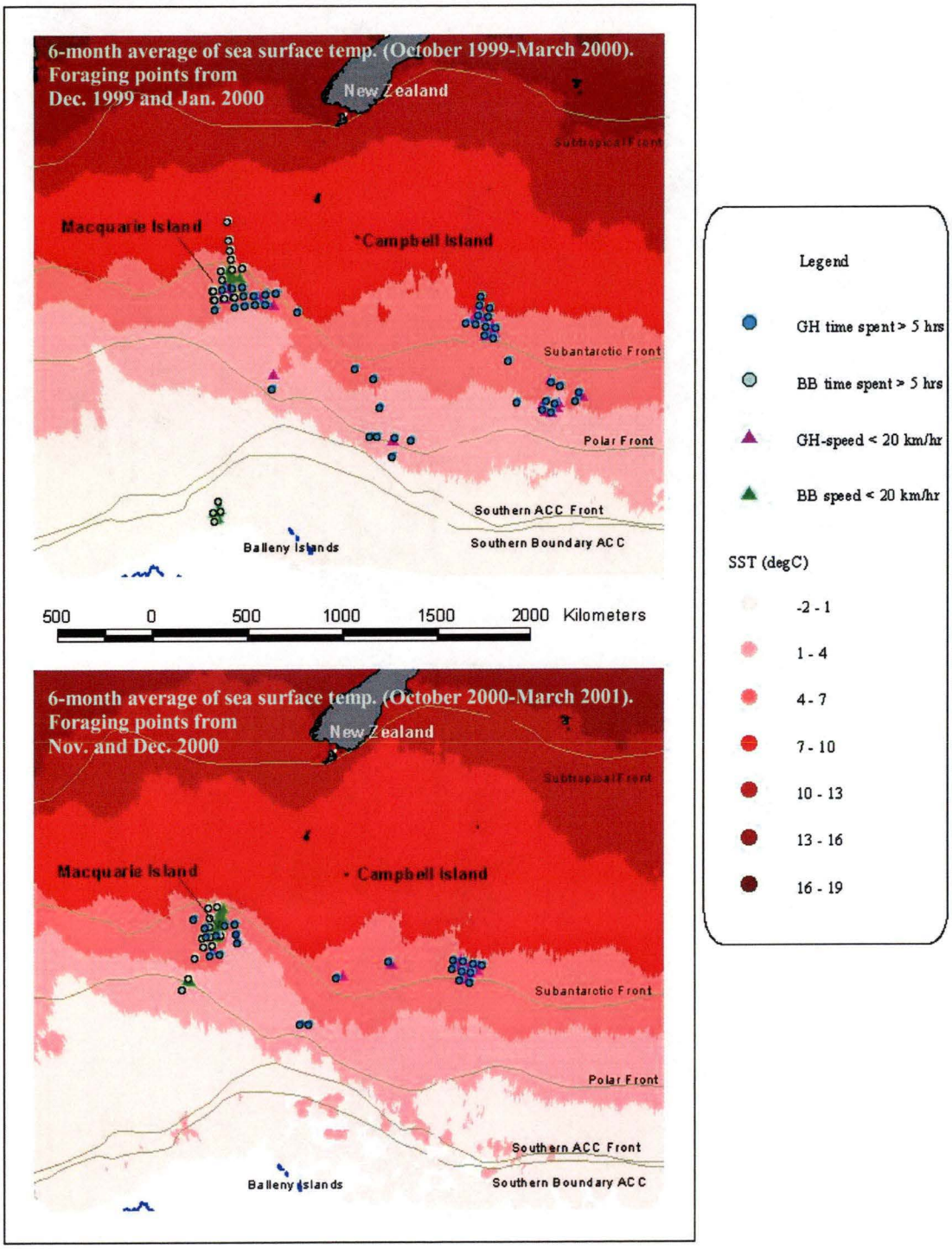


Figure 7.9
Distribution of sea-surface height anomalies and foraging points of Black-browed and Grey-headed albatrosses in waters around Macquarie Island during December 1999 and January 2000. Red areas represent positive anomalies (warmer anti-cyclonic eddies) and blue areas represent negative anomalies (colder cyclonic eddies)

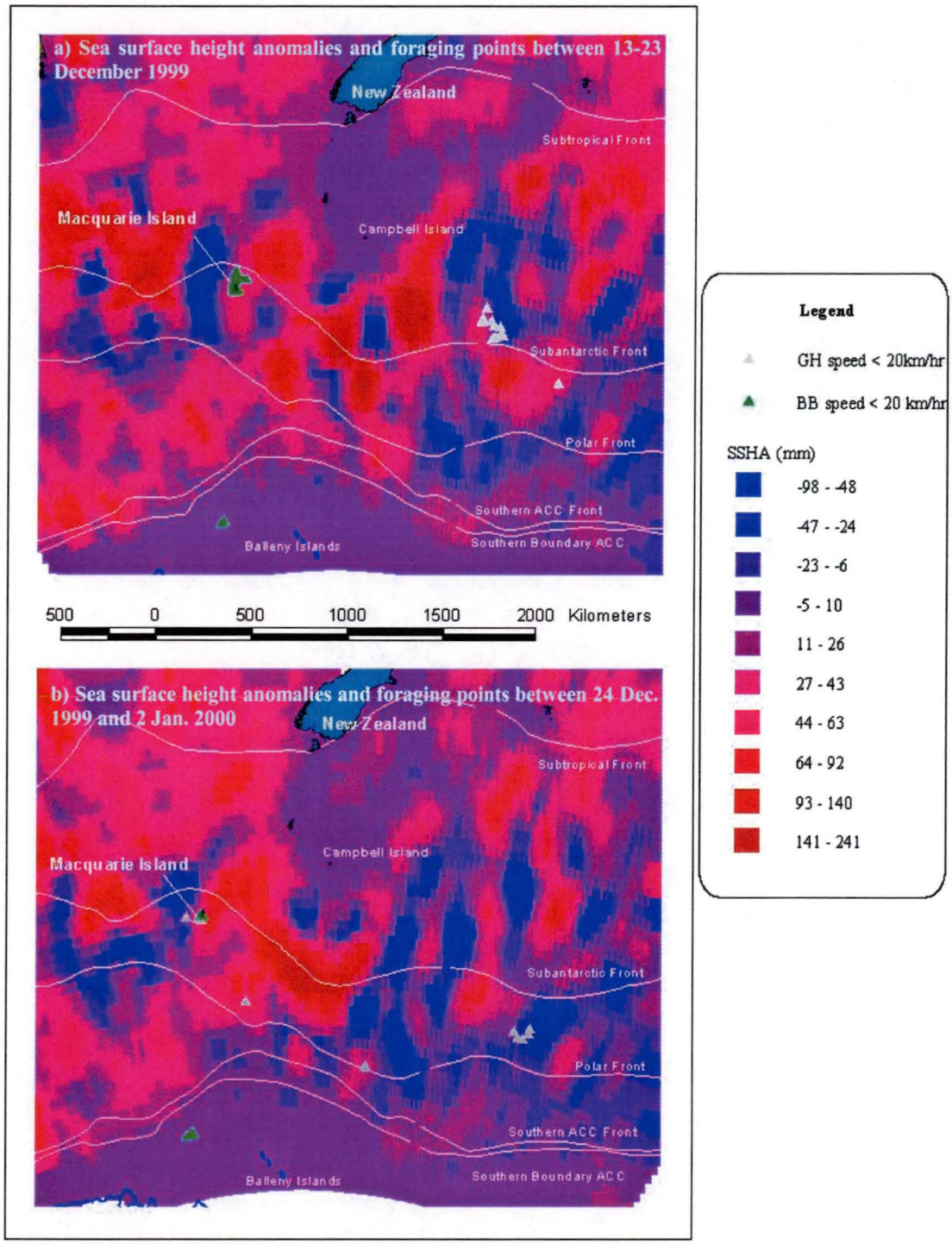
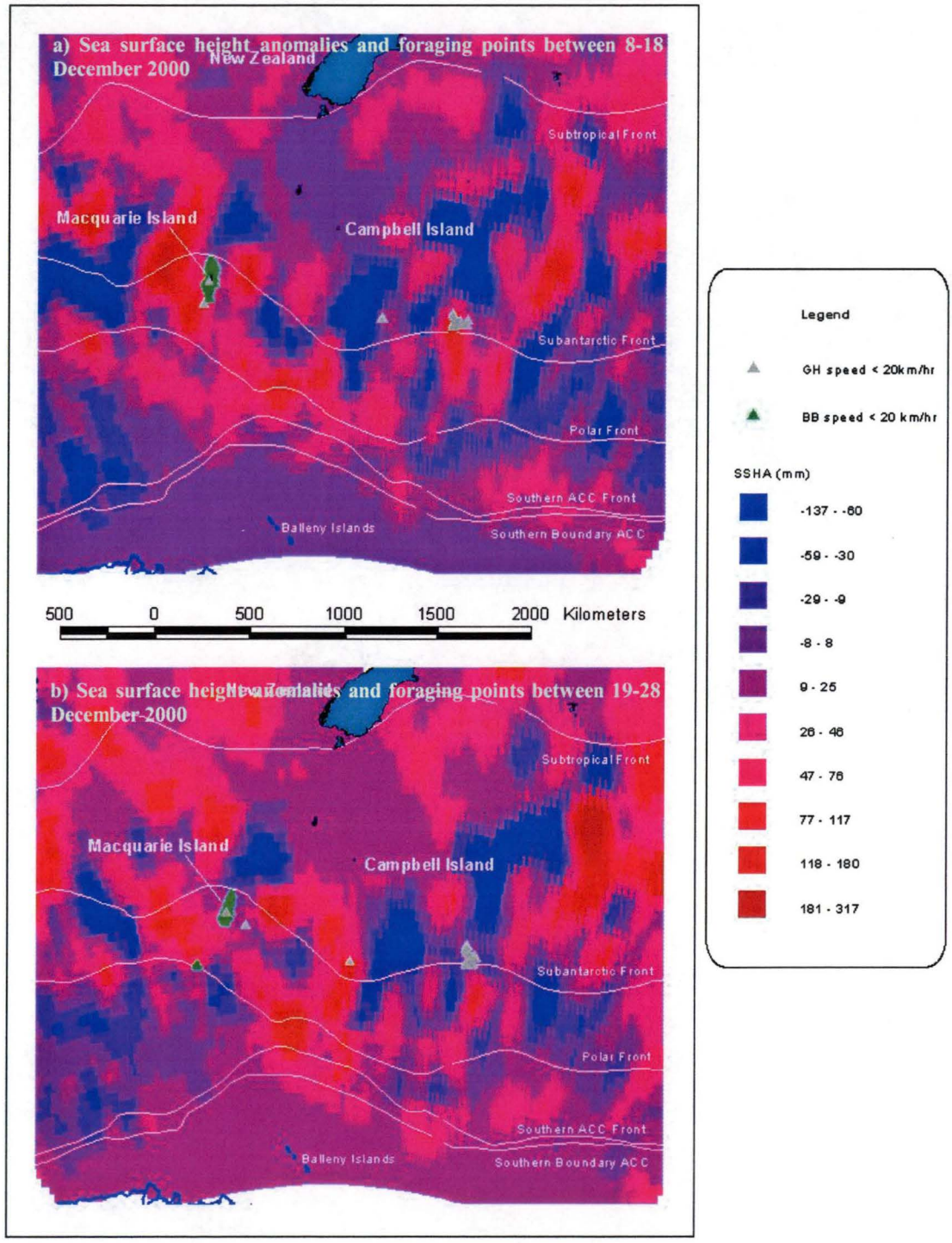


Figure 7.10
Distribution of sea-surface height anomalies and foraging points of Black-browed and Grey-headed albatross in waters around Macquarie Island during December 2000. Red areas represent positive anomalies (warmer anti-cyclonic eddies) and blue areas represent negative anomalies (colder cyclonic eddies)



Due to the neritic nature of most of the Black-browed albatross foraging data, and the concentration of this effort in a relatively small geographic area, it was not possible to comprehensively assess the interactions of this species with anomalies close to Macquarie Island. The foraging points from the longest Black-browed foraging trip (tracked in 1999- Figure 7.9) did not appear to be related to sea-surface height anomalies. Foraging points from the second pelagic foraging trip (tracked in 2000) appeared to be associated with the edges of a positive anomaly close to the Polar Front (Figure 7.10); however, as only two foraging points were obtained on this trip it is not strong evidence of a foraging association with sea-surface height anomalies.

The pelagic foraging trips of the Grey-headed albatrosses appeared to be more associated with sea-surface height anomalies, particularly around the edges of these anomalies. All except two of the pelagic trips were made during the incubation stage. In the first ten day period of 1999 (13-23 December), most of the pelagic foraging points were close to the edges of negative (sensu cold) eddies, or concentrated in a major interface between large positive and negative anomalies to the east of Macquarie Island (Figure 7.9a). In the second ten-day period (immediately following the first - Figure 7.9b) the main foraging areas shifted; however, most foraging points were still observed around the edges of negative anomalies. The two foraging points to the south-east of Macquarie Island were recorded during the brood-guard stage, and both appeared to be associated with positive anomalies. The furthest of these points was associated with a decaying positive anomaly (Figure 7.9b).

A slightly different pattern was observed in the two ten-day periods of the second tracking season (2000/01); however, while not as concentrated as in 1999/00, foraging points were still associated with height anomalies. Most foraging points in the first ten-day period (Figure 7.10a) were associated with the edge and middle of a positive anomaly, with a single point on the edge of a negative anomaly closer to Macquarie Island (Figure 7.10). During the second ten-day period (Figure 7.10b) the foraging locations were in a similar area and it appeared that the positive anomaly had decayed and that the birds were feeding at the interface of two negative anomalies. No foraging points were obtained during the brood-guard stage during this tracking season.

7.3.6 Impact of the PTTs on breeding birds

The PTTs had no discernible impact on breeding birds. After the PTTs were attached, all birds continued to display 'normal' attendance patterns that were consistent with previous breeding seasons. Similarly, there did not appear to be any change in attendance patterns after

the PTTs were removed and there were no nest failures during any of the deployments. Comparisons between the mean shift length of the PTT birds and the mean shift length in each year are shown in Table 7.4.

In general, the shift lengths of birds carrying PTTs and those without were similar. The main exception is the single Black-browed albatross tracked in 1999, which shows higher shift lengths than the mean of the other breeding birds. This could be due to the attachment of the PTT but such conclusions are difficult to draw on the basis of a single bird.

Table 7.4
Mean shift lengths of Black-browed and Grey-headed albatrosses with and without satellite transmitters attached (days ± s.e if more than 1 trip)

Season / status	Black-browed albatross			Grey-headed albatross		
	n	Incubation	Brood	n	Incubation	Brood
1999/00						
with PTT's	1	6.6 (-)	2.2 ± 0.3	3	10.35 ± 0.5	3.5 ± 0.6
without PTT's	137	4.2 ± 0.3	1.6 ± 0.1	41	10.0 ± 0.7	3.3 ± 0.3
2000/01						
with PTT's	2	3.9 ± 0.5	-	2	8.6 ± 0.9	1.5 (-)
without PTT's	86	4.3 ± 0.4	1.7 ± 0.1	50	9.6 ± 0.6	2.4 ± 0.1

One Grey-headed albatross nest failed in 1999 one week after the removal of the PTT. In this case the small, recently unattended chick fell out of the nest and died. A second nest failed in 2000. This chick failed during the brood guard stage and the reasons for the failure are unknown as attendance patterns were normal with frequent changeovers of the parents. There was no evidence to suggest that the PTT deployment and removal had any influence on the failure of these two nests.

7.4 DISCUSSION

7.4.1 Foraging movements and ecology

7.4.1.1 Black-browed albatrosses

Almost all foraging trips by Black-browed albatrosses were within 100 km of Macquarie Island. Most of this neritic foraging effort was concentrated to the north of the island in 1999/00 and spread equally between north and south of the island in 2000/01. Sample sizes in each year were small so it is difficult to draw definitive conclusions from these data. Only one foraging trip spanning hundreds of kilometres was recorded when one female travelled down to 68° S during December 1999. This is consistent with foraging patterns described by Waugh *et al.* (1999a) who described Campbell albatrosses (*Thalassarche impavida*) from Campbell Island covering a large geographic range, extending down to 65°S at times during the breeding season. Other studies have shown that Black-browed albatrosses at South Georgia rarely extend their ranges beyond the shelf and shelf slope waters during the breeding season (Prince *et al.* 1998). However, due to the location of South Georgia (and in contrast to the current study), these waters also lie in the vicinity of the Polar Front.

Although there was some evidence that Black-browed albatrosses from Macquarie Island occasionally utilised resources in the vicinity of the Polar Front, most foraging effort was concentrated in waters around Macquarie Island. Waugh *et al.* (1999a) suggested that the long distance from Campbell Island to the Polar Front was the main reason why the Campbell albatrosses breeding there exhibit higher levels of oceanic foraging than their conspecifics at other sites (geographically closer to the Polar Front). Although Macquarie Island lies on a similar latitude to Campbell Island, due to the pattern of water mixing in the region, it is less than one-third of the distance to the Polar Front (Rintoul et al. 1997). This may in part be responsible for the primarily neritic foraging strategy observed in this study. However, from the available data it appears that whilst Black-browed albatrosses from Macquarie Island utilise a largely neritic foraging strategy during incubation, they are capable of travelling large distances to forage on distant oceanic resources.

Only one Black-browed albatross was tracked during the brood-guard stage and like all other neritic foraging trips recorded, foraging appeared to be concentrated over the ridge complex to the north and south of Macquarie Island. These brood-guard trips were generally shorter than those made during incubation and this is likely to be due to the necessity of delivering food to the chick whilst maintaining it's own body condition (e.g. Weimerskirch *et al.* 1994a).

Waugh *et al.* (1999a) and Prince *et al.* (1998) also described short foraging trips made by Campbell and Black-browed albatrosses to take advantage of productive waters close to land.

7.4.1.3 Grey-headed albatrosses

During incubation most of the tracked Grey-headed albatrosses foraged over two main areas some 1500-2100 km to the east and east south-east of Macquarie Island. These distances are similar to that described by Nel *et al.* (2000), who found that the mean distances travelled by this species breeding on Marion Island was 2182 km. Accurate satellite tracking data (i.e. Location Class 1,2 or 3) showed that birds moved at speeds approaching 90 $kmhr^{-1}$ while travelling to distant foraging locations, and travelling almost invariably began soon after changeover. The rate of travel on the return journey was generally slower, and a less direct route to Macquarie Island was undertaken suggesting that birds may have been prospecting for, and foraging on, more sporadically distributed or patchy resources. Most foraging during incubation was conducted in the vicinity of the Subantarctic Front, in the Polar Frontal Zone and to a lesser extent the Polar Front.

Several foraging trips of Grey-headed albatrosses during the brood-guard stage were also recorded and the differences between these trips and those made during incubation were much greater than those undertaken by Black-browed albatrosses. Brood-guard trips were significantly shorter than incubation trips and foraging effort appeared to be concentrated over the ridge complex to the south of Macquarie Island within 100 km of the coastline. This temporal dichotomy in foraging trips between the incubation and the brood-guard stage was well documented for this species in Chapter 6, and the satellite telemetry data shows that it appears to be highly inter-related with the distances travelled.

7.4.2 Foraging movements and oceanographic features

7.4.2.1 Black-Browed albatrosses

The foraging data of Black-browed albatrosses were examined in conjunction with bathymetry, frontal zones, chlorophyll A levels, sea surface temperatures and sea surface height anomalies. Bathymetry appeared to be one of the most important factors influencing where Black-browed albatrosses from Macquarie Island foraged, with most of the foraging effort concentrated around the ridge complex to the north and south of Macquarie Island. This ridge complex (of which Macquarie Island is the highest point) rises to its highest underwater points to depths of 1000m and is not continuous but is cut in several places by deep passes. To the west of this ridge is a large featureless basin and to the east is the Campbell Plateau, a

relatively shallow extension of the continental shelf from New Zealand (Scott 1994). Even though there is no shelf edge as such around Macquarie Island, the ridge complex to the north and south of the island may support similar levels of production (e.g. see Haney *et al.* 1995, Comiso *et al.* 1993; Moore and Abbott 2000). Antarctic fur seals (*Arctocephalus gazella*) and subantarctic fur seals (*Arctocephalus tropicalis*) breeding on Macquarie Island also spend most of their foraging time on the eastern side of the Macquarie Island ridge to the north of the island (Robinson in press). In fact the main foraging areas of the Black-browed albatrosses and these fur seal species are almost identical suggesting that there are highly productive waters in this area. Further evidence is provided by the main fishing areas of the Australian Licensed Commercial Fishing Vessel, which also targeted the ridge complex to the north of Macquarie Island as this traditionally had one of the highest concentrations of Patagonian Toothfish (Goldsworthy *et al.* 2001).

The tendency of Black-browed albatrosses to forage over neritic waters, usually associated with the shelf edge, has been well documented at South Georgia (Prince *et al.* 1998), Campbell Island (*T. impavida*-Waugh *et al.* 1999a), Iles Kerguelen (Weimerskirch 1998), South Georgia (Prince *et al.* 1998) and the Falkland Islands (Huin 2002). However, all of these studies (with the exception of the latter) tracked breeding birds during the early chick rearing stage and the current study is one of the first to show that this strategy is also utilised during incubation. Long trips during incubation were not always associated with long distances; however two pelagic trips covering hundreds of kilometres were recorded, providing strong evidence that Black-browed albatrosses from Macquarie Island do not only use a solely neritic foraging strategy. It seems likely that the single Black-browed albatross from Macquarie Island that undertook the longest trip did so to utilise resources that were only available in Antarctic waters south of the Antarctic Circumpolar Current. These waters appeared to be rich in chlorophyll A, indicating that such areas are supporting higher levels of primary production. Other pelagic foraging points appeared to be related to the Polar Front, and the interface between sea-surface temperature zones which have also been documented as being associated with higher levels of production (Moore *et al.* 1999; Moore and Abbott 2000).

The temperature zones utilised by Black-browed albatrosses ranged from –2°C to 7°C, which is significantly less than the range of 0°C to 19°C utilised by Campbell albatrosses from Campbell Island and there was little evidence that the foraging areas of this species were associated with sea surface height anomalies. Many of the oceanographic features described here are inextricably linked. For example bathymetric features influence ocean currents that cause sea-surface height anomalies to form and subsequently influence chlorophyll A levels.

oceanic hydrology (Wilson and Adamec 2001), sea-surface temperatures and frontal zones are similarly inter-related (Moore *et al.* 1999; Trull *et al.* 2001) and consequently identifying the primary factor driving the location of the Black-browed foraging areas is difficult. Nevertheless, it appears that the shelf-like waters above the Macquarie Ridge are the most influential factor, followed by chlorophyll levels, sea-surface temperatures, frontal zones and sea surface height anomalies.

7.4.2.2 Grey-headed albatrosses

There are similar difficulties in identifying the oceanic features that influenced the foraging ecology of the Grey-headed albatrosses. However, this species appears to preferentially target different features, which is likely to be related to different preferred prey items. Bathymetry appeared to play a much less important role in the areas targeted by Grey-headed albatrosses during incubation since most foraging occurs over deep, relatively featureless waters to the east of the Campbell Plateau in the vicinity of the Subantarctic Front, the Polar Frontal Zone and the Polar Front. These waters are rich in evolving and decaying sea-surface height anomalies and most foraging was concentrated at the edges of these anomalies or at the interface of two anomalies. This is very similar to the foraging strategies of Grey-headed albatrosses on pelagic trips from Marion Island and South Georgia where birds preferentially foraged around warm eddies in the Polar Frontal Zone (Nel *et al.* 2001; Rodhouse *et al.* 1996). Both positive and negative anomalies were targeted, often in the vicinity of frontal zones and were particularly associated with high gradients in sea-surface temperatures.

The temperature range of waters utilised by Grey-headed and Black-browed albatrosses from Macquarie Island were relatively similar and birds rarely foraged in the warmer waters of the Subantarctic Front. This is in contrast to the findings of Waugh *et al.* (1999a) who described Grey-headed albatrosses from Campbell Island utilising waters with warmer sea-surface temperatures ranging from 3°C to 15°C. This may be attributable in part to the slightly more northerly location of Campbell Island compared to Macquarie Island, or the differences in the distances to the Subantarctic and Polar Front (Rintoul *et al.* 1997). Grey-headed albatrosses from South Georgia tracked during chick rearing also foraged over a broad geographic range, covering a high range of temperature zones (Prince *et al.* 1998). There was little evidence to suggest that the foraging areas of Grey-headed albatrosses were associated with high chlorophyll levels, perhaps reflecting the higher position of the preferred prey items on the food chain.

During early chick rearing the foraging strategy changed significantly with more effort focussed on the ridge complex to the south and off the west coast of Macquarie Island. It is likely that due to the nutritional requirements of the chick, parents have less choice in the feeding grounds they utilise and therefore few long trips during the brood-guard were recorded. The pelagic trips that were tracked during the brood-guard still appeared to target the edges of anomalies and the Polar Front; however the duration of foraging time at these locations appeared to be much reduced.

7.4.2.3 Prey, oceanography and resource partitioning

No diet samples were collected from tracked birds so it was difficult to define clear correlations between the oceanographic features targeted and the prey items associated with them. The predominance of Black-browed albatrosses feeding on the shelf edges and other high nutrient waters suggests that Black-browed albatrosses are feeding on prey-items that are lower down the food chain (and therefore assumed to be more closely correlated with chlorophyll A levels) than Grey-headed albatrosses. Several studies have documented the strong relationship between Black-browed albatrosses from South Georgia and krill (e.g. Croxall *et al.* 1997; Croxall *et al.* 1999b; Nevitt 1999) while Waugh *et al.* 1999a and Cherel *et al.* 2000 showed that small myctophid fish predominated in the diets of Campbell and Black-browed albatrosses during early chick rearing on Campbell Island and Iles Kerguelen.

Antarctic and Subantarctic fur seals breeding on Macquarie Island foraging in very similar locations to Black-browed albatrosses predominantly consume small myctophid fish (S. Robinson, in press). It is possible that Black-browed albatrosses from Macquarie Island are preferentially targeting similar prey items throughout incubation and the brood-guard stage and this allows them to forage close to the island for much of the time.

In a review of the diet of albatrosses Cherel and Klages (1998) reported that Black-browed albatrosses from some locations preferentially fed on squid and Cherel *et al.* (2000) reported that squid constituted about 10% of the diet of Black-browed albatrosses from Iles Kerguelen. The few longer trips observed by Black-browed albatrosses during incubation suggest that the food resources around Macquarie Island may at times be insufficient and therefore longer trips are required to find more oceanic prey items.

The marked differences in the foraging strategies and geographic areas of the Grey-headed and Black-browed albatrosses from Macquarie Island suggest that the two species are feeding on different prey items and there is a clear segregation of resources utilised, particularly

during incubation. Such differences were clearly identified by Cherel and Klages (1998) and Veit and Prince (1997) showed that Black-browed albatrosses responded much more strongly than Grey-headed albatrosses to krill. Rodhouse *et al.* (1996) described large stocks of squid in the Polar Frontal Zone in the Scotia Sea and suggested that Grey-headed albatrosses foraging in this area were preferentially targeting squid as a prey item. These authors also suggested that squid were associated with warm eddies in this area. Squid has been identified as a major component of the diet in most studies on the feeding ecology of this species (e.g. Prince 1980; Cherel and Klages 1998; Waugh *et al.* 1999a; Nel *et al.* 2000; Nel *et al.* 2001) and in this context, there is evidence from the data on foraging locations to suggest that Grey-headed albatrosses breeding on Macquarie Island also target specific areas to maximise the yield of these type of prey.

7.4.3 Foraging movements, fisheries and the Marine Park

The amount of time spent by Black-browed and Grey-headed albatrosses in the Australian Economic Exclusion Zone (EEZ) around Macquarie Island and CCAMLR Statistical Sub-area 88.1 were quantified and both species were observed to spend significant proportions of their foraging times in these zones. The only sanctioned fishery operating in the Macquarie Island EEZ is trawling for Patagonian Toothfish. This fishery began in 1994 and has continued annually to the present day (2000/01 summer). Several restrictions are placed on this concession by the Australian Fisheries Management Authority (AFMA) including: mandatory carriage of two observers with each vessel, that the vessel is fitted with a Vessel Monitoring System (VMS) and that no fish offal be discharged from the vessel (Robinson and Scott 1999). The fishing method is restricted to pelagic or demersal trawling and long-line fishing is prohibited in the EEZ around Macquarie Island because of the vulnerability of the threatened albatrosses to the fishing method. All fishing is prohibited in the state controlled waters, which extend three nautical miles from Macquarie Island.

The overlap observed in the foraging areas of the Black-browed albatrosses and the areas fished is probably due to a combination of two factors. Firstly it seems likely that Patagonian Toothfish also target the highly productive area to the north and therefore fisheries also target these areas (Goldsworthy *et al.* 2001). Secondly, several studies have shown that Black-browed albatrosses, like many species of seabird are attracted to fishing vessels (Cherel *et al.* 1996; Gales *et al.* 1998; Weimerskirch *et al.* 2000b) and observer reports from the ALCFV indicate that Black-browed albatrosses from Macquarie Island are second only to Northern giant petrels (*Macronectes halli*) as the most abundant seabird attending the vessel (AFMA fisheries observers, personal communication)

Roberston and Weinecke (2001) suggested that there was little incidental mortality of seabirds associated with the fishery around Macquarie Island; however, it is possible that negative effects of this fishery manifest themselves in other ways. For example, breeding birds attending the fishing vessel may be distracted from their normal foraging routine and consequently shift lengths may become longer than usual. Longer shift lengths of this species are negatively correlated with breeding success (Chapter 6 – Section 6.3.4). In addition, the number of fishing days on which Toothfish were caught has decreased from over 70 in the first two years of fishing to under thirty in 1999/00 and 2000/01 (Geoff Tuck and Tim Lamb, unpublished data) suggesting that Toothfish numbers have declined. Given the significance of this species in the ecosystem around Macquarie Island (Goldsworthy *et al.* 2001) such perturbations to the ecosystem may have serious implications for the other members of this complexly inter-related food chain.

Anther area of significant concern in relation to fisheries around Macquarie Island is CCAMLR Statistical Sub-area 88.1. The area is classified as an 'average risk' Statistical Sub-area and 'at-risk' seabird numbers in this area were thought to be low (SC-CAMLR-XX, 2001-Table 63). The number of hooks set in this area has increased annually since 1996/97 to 1.5 million hooks set in the 2000/01 split year (SC-CAMLR-XIX 2000, SC-CAMLR-XX 2001). Hook numbers seem likely to rise in the future with fishing vessels based in South Africa, New Zealand, Japan and Russia applying for permission to fish in this area in the 2002/03 (SC-CAMLR-XX 2001-Table 63). In addition to these sanctioned vessels it is likely that the area is utilised by illegal fisheries and concerns must be raised about the potential for negative interactions with vulnerable seabirds, particularly in light of the foraging areas of the Black-browed and Grey-headed albatrosses from Macquarie Island. Information from this study will be valuable in the review of risk assessments undertaken by IMALF each year.

Foraging data on Black-browed and Grey-headed albatrosses from Macquarie Island will also be useful in a review of the boundaries and zone classification of the Macquarie Island Marine Park. Both species spend almost half of their foraging time within the Macquarie Island EEZ, but outside of the Marine Park area. Consequently the current boundaries and zonation of the Marine Park fail to adequately protect the main foraging areas of these populations, particularly given their small and vulnerable population status nature of the breeding populations. A timely review of the Marine Park boundaries in light of the albatross foraging data obtained here would allow decisions regarding fisheries management strategies in the vicinity of Macquarie Island to be more soundly based.

Appendix 7.1
Duration of PTT deployment and proportion of hits excluded in each location class after fitering for speeds < 90 km/hr

PTT ID	Duration of deployment (days)	Percentage of location class hits excluded by filtering for speeds < 90 km/hr						
		3	2	1	0	A	B	All
Black-browed albatross								
20876_99	18.7	0	0	4	11	14	29	58
20875_00	18.3	0	0	0	4	3	26	32
20877_00	9.2	0	0	2	4	8	18	31
Mean	15.4	0	0	2	6	8	24	41
Grey-headed albatross								
20874_99	13.5	0	0	5	9	9	14	37
20875_99	14.8	0	0	3	15	9	19	46
20877_99	16.6	0	0	0	18	15	18	51
20874_00	11.1	-	0	3	8	7	20	39
20876_00	7.5	0	0	2	5	5	10	22
Mean	13	0	0	3	11	9	16	39
Overall mean	13.9	0	0	2	9	9	19	40

Appendix 7.2
Number and proportion of filtered hits in each location class (foraging data only)

PTT ID	# hits in each location class						Total hits	% hits in each location class					
	3	2	1	0	A	B		3	2	1	0	A	B
Black-browed albatross													
20876_99	1	1	29	127	30	17	205	0	0	14	62	15	8
20875_00	0	3	15	96	29	17	160	0	2	9	60	18	11
20877_00	0	0	7	61	13	8	89	0	0	8	69	15	9
2000/01 total	0	3	22	157	42	25	249	0	2	9	63	17	10
Overall total	1	4	51	284	72	42	454	0	1	11	63	16	9
Grey-headed albatross													
20874_99	0	0	7	53	21	19	100	0	0	7	53	21	19
20875_99	0	1	9	75	16	24	125	0	1	7	60	13	19
20877_99	0	2	3	12	2	2	21	0	10	14	57	10	10
1999/00 total	0	3	19	140	39	45	246	0	1	8	57	16	18
20874_00	0	1	5	30	19	26	81	0	1	6	37	23	32
20876_00	1	0	10	41	13	15	80	1	0	13	51	16	19
2000/01 total	1	1	15	71	32	41	161	1	1	9	44	20	25
Overal total	1	4	34	211	71	86	407	0	1	8	52	17	21
Both species total	2	8	85	495	143	128	861	0.23	0.93	9.87	57.5	16.6	14.9

Appendix 7.3
Summary of filtered satellite telemetry data, Black-browed and Grey headed albatrosses during December and January 1999 and November and December 2000

Bird	Bird ID	sex	trip #	foraging area	stage	leave	arrive	duration	notes
1999									
Grey-headed albatross, A0409, male, Age = 22 + years, PTT ID-20877_99 Deployment period - 20/12/99 to 19/1/00			1	pelagic	Incubation	26/12/1999 12 03	06/01/2000 05 00	10 7	changed over and headed south-east through the polar frontal zone until it hit the polar front approximately 1200 km se Macquarie Island (covered this distance in approx 30 hrs at speeds of an average speed of 60-70 km/hr. then spent approximately 3 5 days foraging in a circle 160km across 1700 km east south east mi once out of this circle bird spent
			2	pelagic	brood/guard	10/01/2000 04 15	13/01/2000 20 18	3 7	changed over and headed south-east at high speed (around 70km hr) to the pf, 1100km away from Macquarie Is (took 14 hrs) Foraged between the pf and Southern Antarctic Circumpolar Current Front for a day before returning to Macquarie Island along a similar route, but at slower speed (48 hrs to cover the return 1100 km Closely followed the sub-antarctic front on its return journey
			3	neritic	brood/guard	16/01/2000 16:11	18/01/2000 20:05	2 2	Foraged to the south and west of Macquarie Island at speeds less than 30 km, mean =17+-10km/hr, mostly within 30km/hr, furthest out was 50 km/hr
Black-browed albatross, 121-39117, female, age = 12+ years, PTT ID - 20876_99: Deployment period - 20/12/99 to 20/1/00			1	pelagic	incubation	26/12/1999 21 54	02/01/2000 12 48	6 6	headed 325 km to north Macquarie Island in first 12 hrs after changeover, then turned around and headed 360 km south west then 1300 due south over 1 5 days, up to speeds in excess of 90 km/hr, foraged at this location for 2 5 days, then followed original track due north until it hit the polar front then headed north-west back to breeding site on MI
			2	neritic	brood/guard	03/01/2000 17 15	05/01/2000 08 18	1 6	foraged north at relatively low speed 20-50 km/hr to 200km north Macquarie Island then headed back at same pace, all hits over ridge complex
			3	neritic	brood/guard	06/01/2000 14 35	08/01/2000 09 40	1 8	for first 24 hrs stayed south within 10-20 km of breeding site, then quickly traveled up N, foraged there for a few hrs and headed back
			4	neritic	brood/guard	09/01/2000 11 53	10/01/2000 14 14	1 1	in first 12 hrs headed north (100 km north from mi) then north-east (190 km north-east mi) over the ridge complexes to the north and e of Macquarie Island then head back south and stayed within 10-20 km Macquarie Island before changing over again
			5	neritic	brood/guard	11/01/2000 11 08	14/01/2000 05 11	2 8	possibly 2 foraging trips with very quick changeover First up headed north foraging mainly around 40km north Macquarie Island but venturing as far as 100km n/north-east back within 5km of nest site in 24hrs, hung around there for 5-6 hrs before heading off again to forage 20 km due w Macquarie Island for 6-8 hrs then back to southern end for few hrs before changing over
			6	neritic	brood/guard	15/01/2000 05 02	17/01/2000 20 24	2 6	possibly 2 foraging trips changed over first thing, headed straight up n, foraged 40-60 km north Macquarie Island on ridge complex, headed back down south overnight, spent first half 16th there (within 10km breeding site) before heading north again (same area) 24 hrs later
			7	neritic	brood/guard	18/01/2000 12 42	20/01/2000 17 00	2 2	headed n, foraged over ridge 40-70 km to north for 1 5 days then headed south and changed over

Appendix 7.3
Summary of filtered satellite telemetry data, Black-browed and Grey headed albatrosses during December and January 1999 and November and December 2000

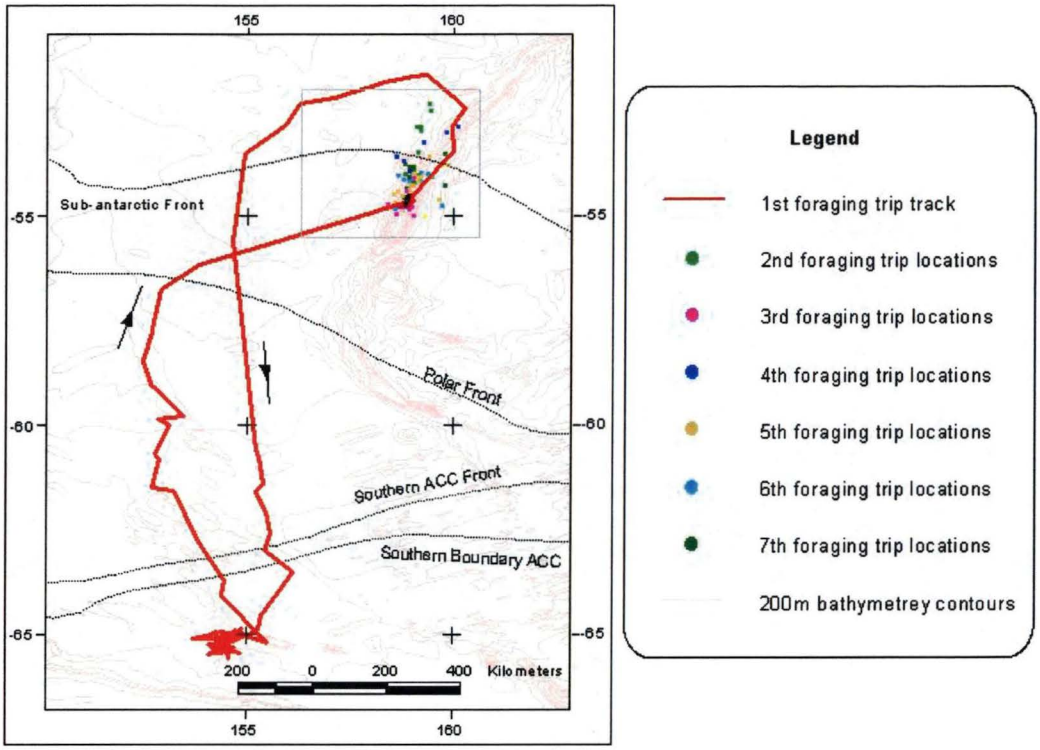
Bird	Bird ID	sex	trip #	foraging area	stage	leave	arrive	duration	notes
1999									
Grey-headed albatross, A0409, male, Age = 22 + years, PTT ID-20877_99 Deployment period - 20/12/99 to 19/1/00			1	pelagic	Incubation	26/12/1999 12:03	06/01/2000 05 00	10 7	changed over and headed south-east through the polar frontal zone until it hit the polar front approximately 1200 km se Macquarie Island (covered this distance in approx 30 hrs at speeds of an average speed of 60-70 km/hr then spent approximately 3 5 days foraging in a circle 160km across 1700 km east south east mi once out of this circle bird spent
			2	pelagic	brood/guard	10/01/2000 04 15	13/01/2000 20 18	3.7	changed over and headed south-east at high speed (around 70km hr) to the pf, 1100km away from Macquarie Is (took 14 hrs) Foraged between the pf and Southern Antarctic Circumpolar Current Front for a day before returning to Macquarie Island along a similar route, but at slower speed (48 hrs to cover the return 1100 km Closely followed the sub antarctic front on its return journey
			3	neritic	brood/guard	16/01/2000 16.11	18/01/2000 20 05	2 2	Foraged to the south and west of Macquarie Island at speeds less than 30 km, mean =17+-10km/hr, mostly within 30km/hr, furthest out was 50 km/hr
Black-browed albatross, 121-39117, female, age = 12+ years, PTT ID - 20876_99: Deployment period - 20/12/99 to 20/1/00			1	pelagic	incubation	26/12/1999 21 54	02/01/2000 12 48	6 6	headed 325 km to north Macquarie Island in first 12 hrs after changeover, then turned around and headed 360 km south west then 1300 due south over 1 5 days, up to speeds in excess of 90 km/hr, foraged at this location for 2 5 days, then followed original track due north until it hit the polar front then headed north-west back to breeding site on MI
			2	neritic	brood/guard	03/01/2000 17 15	05/01/2000 08 18	1 6	foraged north at relatively low speed 20-50 km/hr to 200km north Macquarie Island then headed back at same pace, all hits over ridge complex
			3	neritic	brood/guard	06/01/2000 14 35	08/01/2000 09 40	1 8	for first 24 hrs stayed south within 10-20 km of breeding site, then quickly traveled up N, foraged there for a few hrs and headed back
			4	neritic	brood/guard	09/01/2000 11 53	10/01/2000 14 14	1 1	in first 12 hrs headed north (100 km north from mi) then north-east (190 km north-east mi) over the ridge complexes to the north and e of Macquarie Island then head back south and stayed within 10-20 km Macquarie Island before changing over again
			5	neritic	brood/guard	11/01/2000 11 08	14/01/2000 05.11	2 8	possibly 2 foraging trips with very quick changeover First up headed north foraging mainly around 40km north Macquarie Island but venturing as far as 100km n/north-east back within 5km of nest site in 24hrs, hung around there for 5-6 hrs before heading off again to forage 20 km due w Macquarie Island for 6-8 hrs then back to southern end for few hrs before changing over
			6	neritic	brood/guard	15/01/2000 05 02	17/01/2000 20 24	2 6	possibly 2 foraging trips changed over first thing, headed straight up n, foraged 40-60 km north Macquarie Island on ridge complex, headed back down south overnight, spent first half 16th there (within 10km breeding site) before heading north again (same area) 24 hrs later
			7	neritic	brood/guard	18/01/2000 12 42	20/01/2000 17 00	2 2	headed n, foraged over ridge 40-70 km to north for 1 5 days then headed south and changed over

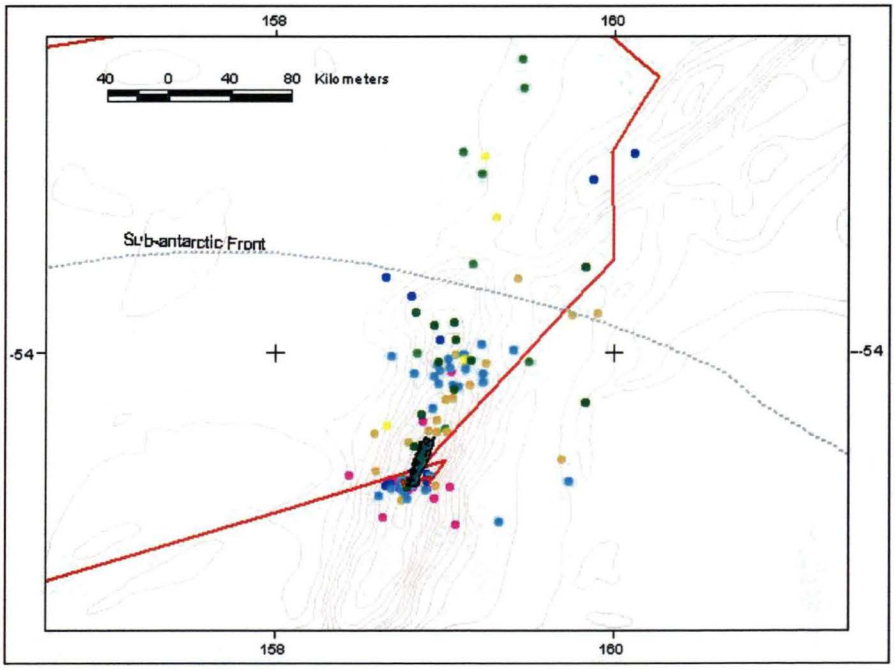
Appendix 7.3
Summary of filtered satellite telemetry data, Black-browed and Grey headed albatrosses during December and January 1999 and November and December 2000

Bird	Bird ID	sex	trip #	foraging area	stage	leave	arrive	duration	notes
1999									
Grey-headed albatross, A0409, male, Age = 22 + years, PTT ID-20877_99 Deployment period - 20/12/99 to 19/1/00			1	pelagic	Incubation	26/12/1999 12 03	06/01/2000 05 00	10 7	changed over and headed south-east through the polar frontal zone until it hit the polar front approximately 1200 km se Macquarie Island (covered this distance in approx 30 hrs at speeds of an average speed of 60-70 km/hr then spent approximately 3 5 days foraging in a circle 160km across 1700 km east south east mi once out of this circle bird spent
			2	pelagic	brood/guard	10/01/2000 04 15	13/01/2000 20.18	3 7	changed over and headed south-east at high speed (around 70km hr) to the pf, 1100km away from Macquarie Is (took 14 hrs) Foraged between the pf and Southern Antarctic Circumpolar Current Front for a day before returning to Macquarie Island along a similar route, but at slower speed (48 hrs to cover the return 1100 km Closely followed the sub antarctic front on its return journey
			3	neritic	brood/guard	16/01/2000 16.11	18/01/2000 20.05	2 2	Foraged to the south and west of Macquarie Island at speeds less than 30 km, mean =17+-10km/hr, mostly within 30km/hr, furthest out was 50 km/hr
Black-browed albatross, 121-39117, female, age = 12+ years, PTT ID - 20876_99: Deployment period - 20/12/99 to 20/1/00			1	pelagic	incubation	26/12/1999 21 54	02/01/2000 12 48	6 6	headed 325 km to north Macquarie Island in first 12 hrs after changeover, then turned around and headed 360 km south west then 1300 due south over 1 5 days, up to speeds in excess of 90 km/hr, foraged at this location for 2.5 days, then followed original track due north until it hit the polar front then headed north-west back to breeding site on MI
			2	neritic	brood/guard	03/01/2000 17 15	05/01/2000 08 18	1 6	foraged north at relatively low speed 20-50 km/hr to 200km north Macquarie Island then headed back at same pace, all hits over ridge complex
			3	neritic	brood/guard	06/01/2000 14 35	08/01/2000 09 40	1 8	for first 24 hrs stayed south within 10-20 km of breeding site, then quickly traveled up N, foraged there for a few hrs and headed back
			4	neritic	brood/guard	09/01/2000 11 53	10/01/2000 14 14	1 1	in first 12 hrs headed north (100 km north from mi) then north-east (190 km north-east mi) over the ridge complexes to the north and e of Macquarie Island then head back south and stayed within 10-20 km Macquarie Island before changing over again
			5	neritic	brood/guard	11/01/2000 11 08	14/01/2000 05 11	2 8	possibly 2 foraging trips with very quick changeover First up headed north foraging mainly around 40km north Macquarie Island but venturing as far as 100km n/north-east back within 5km of nest site in 24hrs, hung around there for 5-6 hrs before heading off again to forage 20 km due w Macquarie Island for 6-8 hrs then back to southern end for few hrs before changing over
			6	neritic	brood/guard	15/01/2000 05 02	17/01/2000 20 24	2 6	possibly 2 foraging trips changed over first thing, headed straight up n, foraged 40-60 km north Macquarie Island on ridge complex, headed back down south overnight, spent first half 16th there (within 10km breeding site) before heading north again (same area) 24 hrs later
			7	neritic	brood/guard	18/01/2000 12 42	20/01/2000 17 00	2 2	headed n, foraged over ridge 40-70 km to north for 1 5 days then headed south and changed over

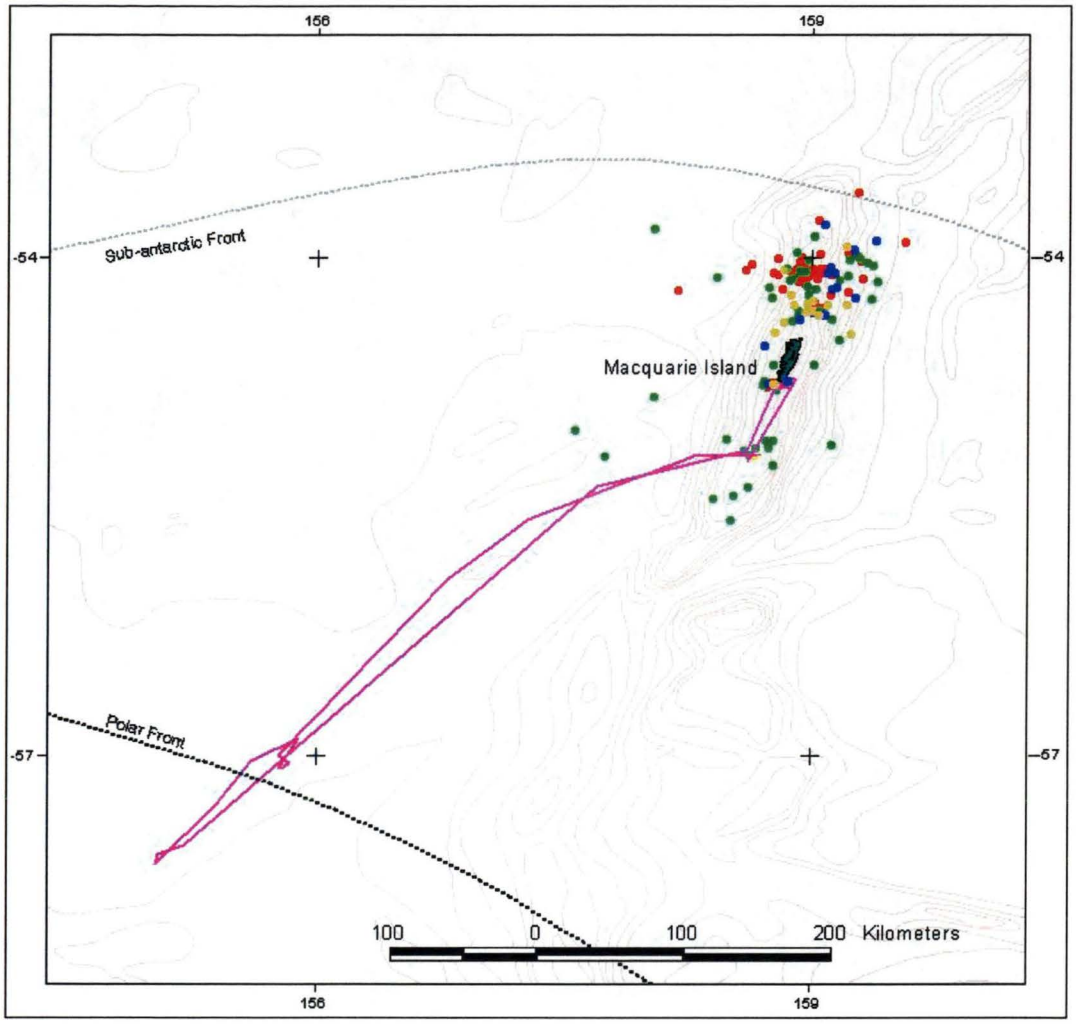
Appendix 7.4

Foraging track of female Black-browed albatross in December 1999 and January 2000. PTT_ID – BB_876_99





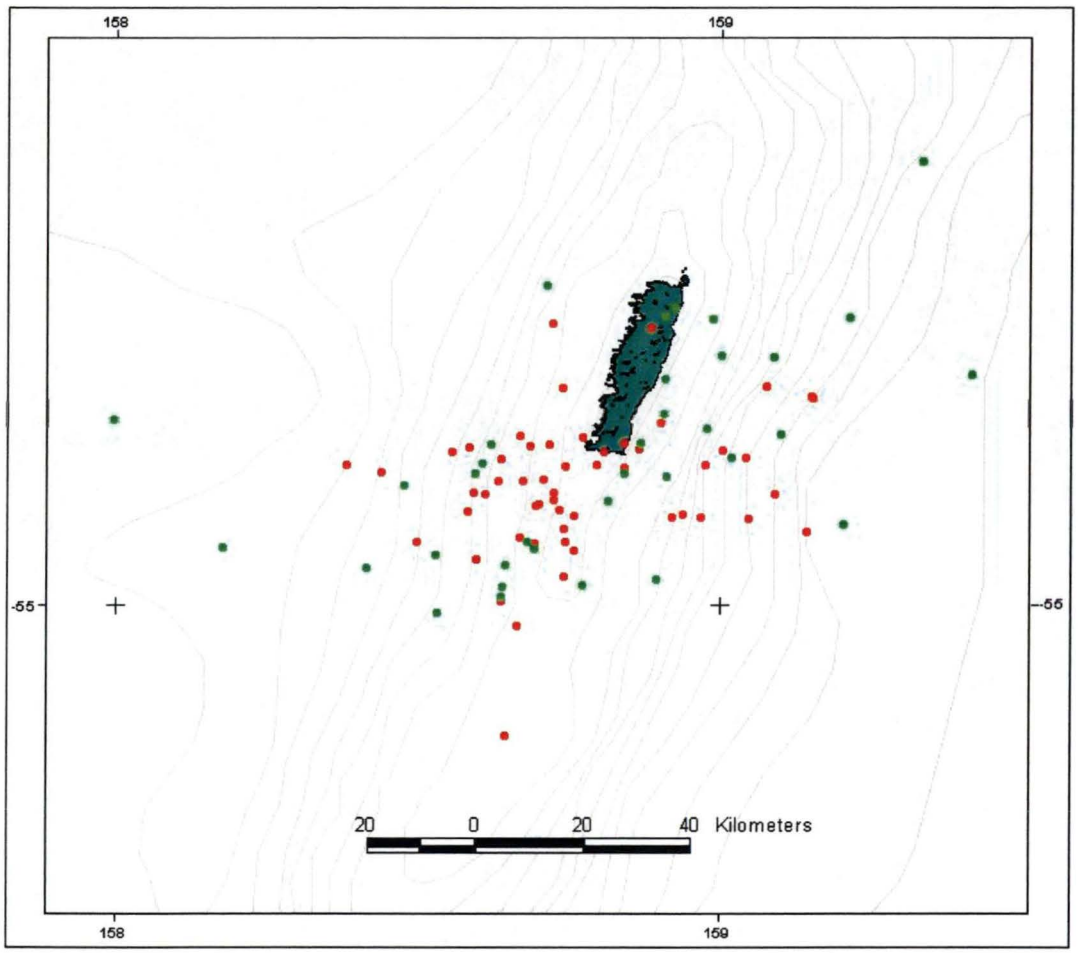
Appendix 7.5
Foraging track of male Black-browed albatross in November and December 2000.
PTT_ID – BB_875_00

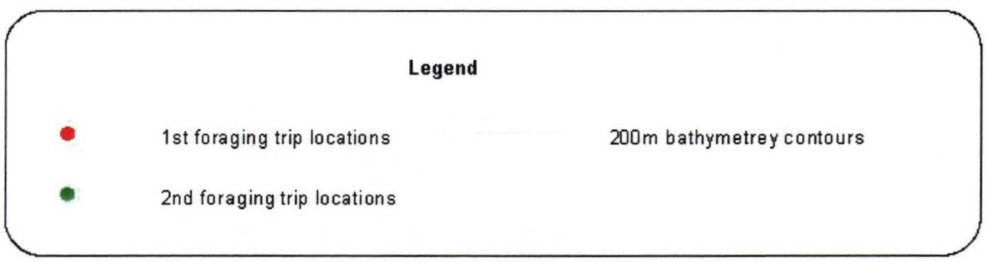


Legend

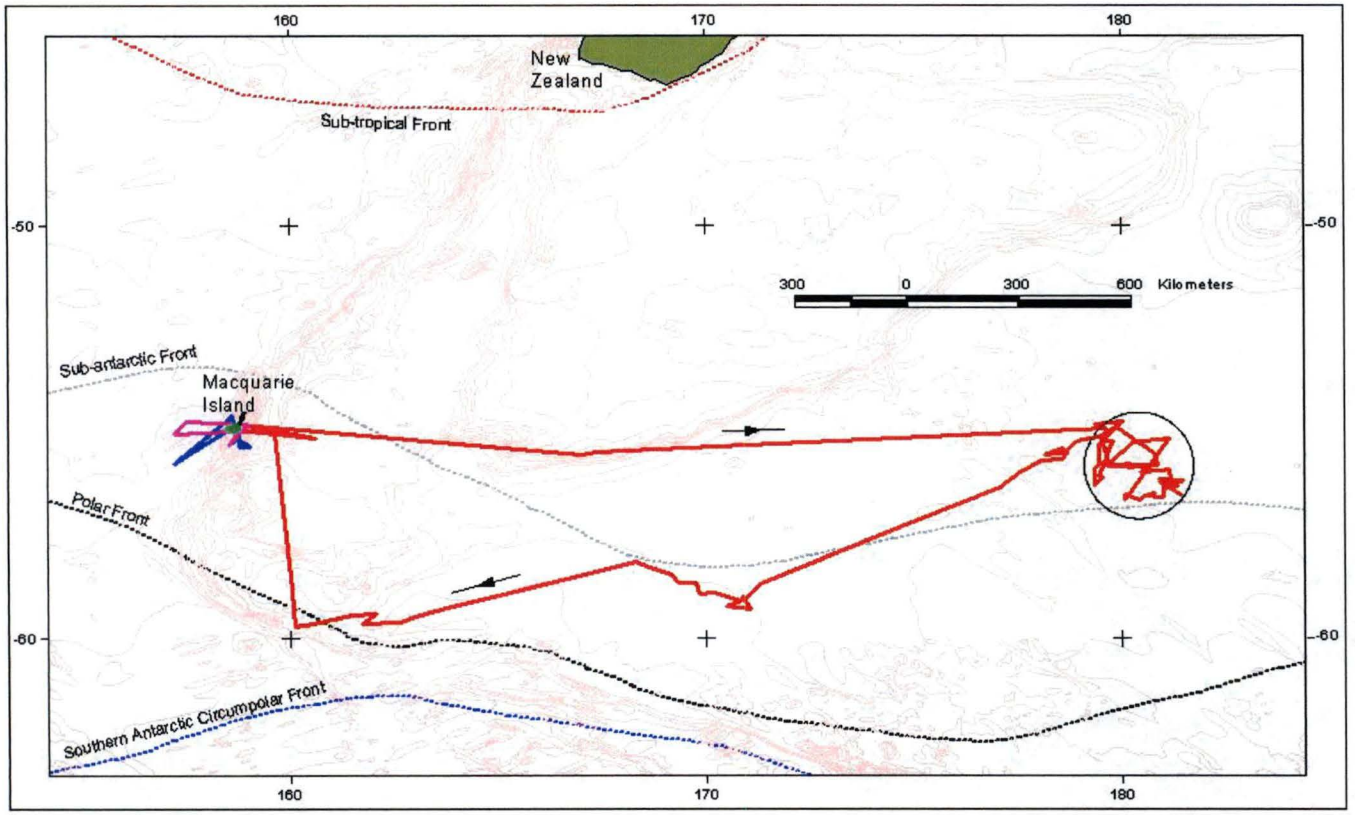
- 1st foraging trip locations
- 2nd foraging trip locations
- 3rd foraging trip
- 4th foraging trip locations
- 5th foraging trip
- 200m bathymetrey contours

Appendix 7.6
Foraging track of female Black-browed albatross in November and December 2000. PTT_ID – BB_877_00





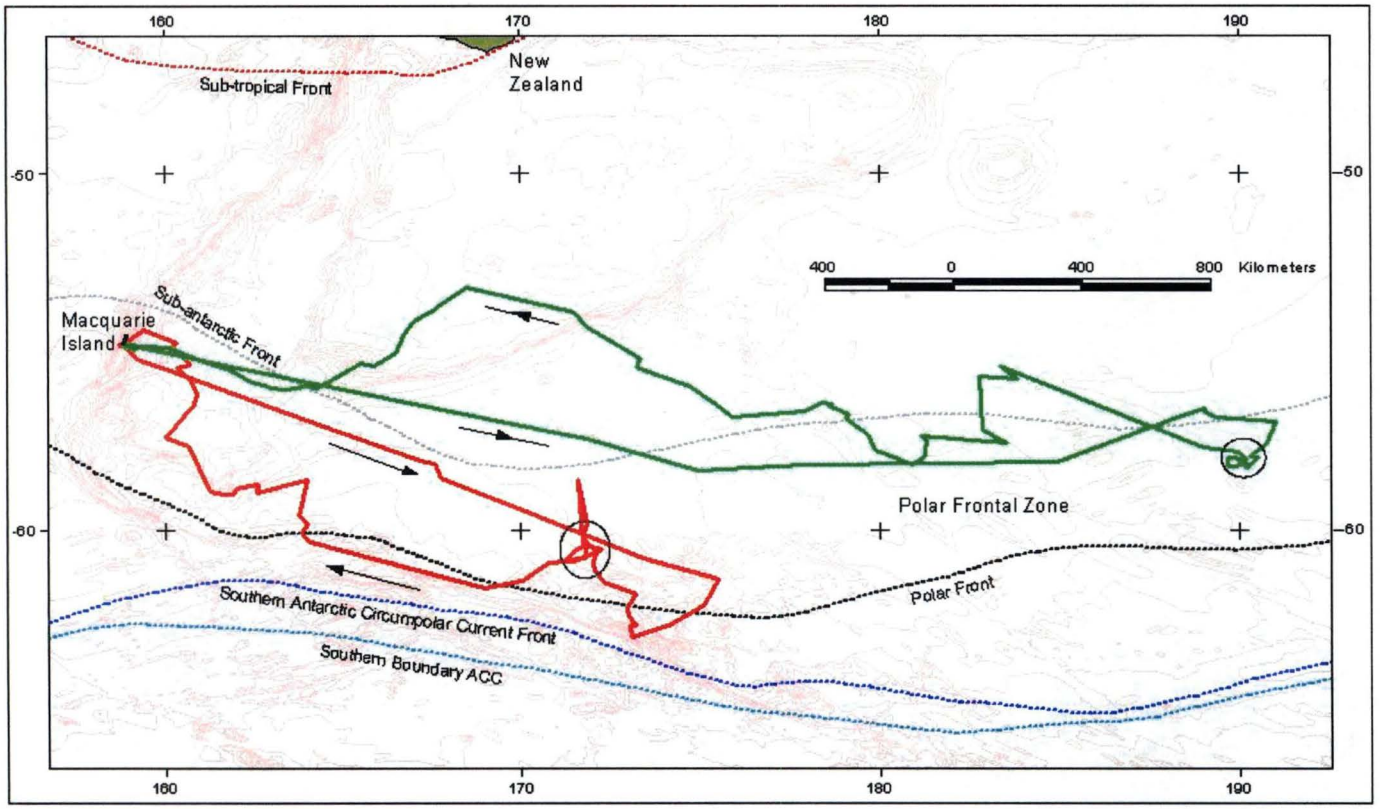
Appendix 7.7
Foraging track of female Grey-headed albatross in December 1999 and January 2000.
PTT_ID – GH_874_99



Legend

1st foraging trip
2nd foraging trip
3rd foraging trip
4th foraging trip
200m Bathymetry contours
foraging area

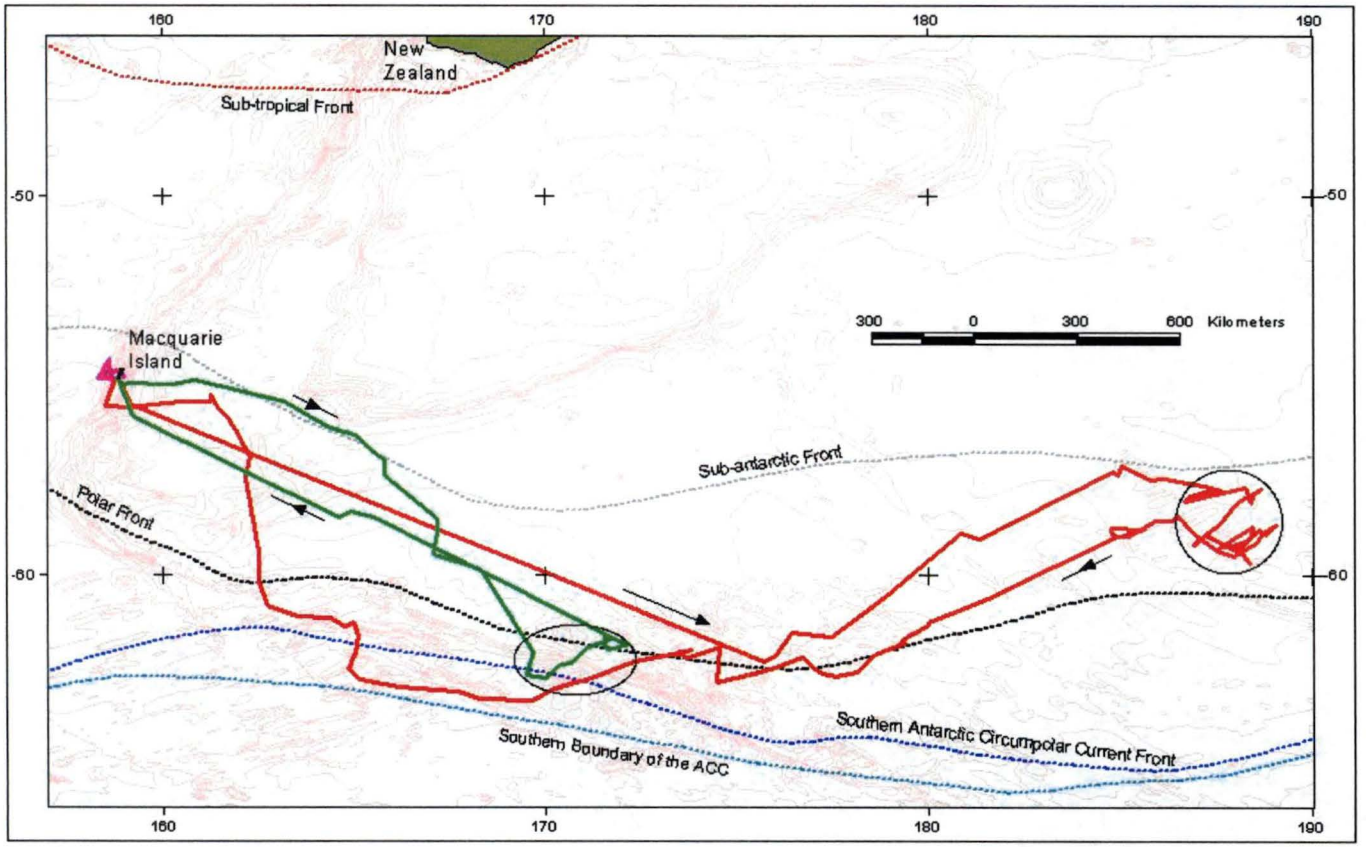
Appendix 7.8
Foraging track of female Grey-headed albatross in December 1999 and January 2000.
PTT_ID – GH_875_99



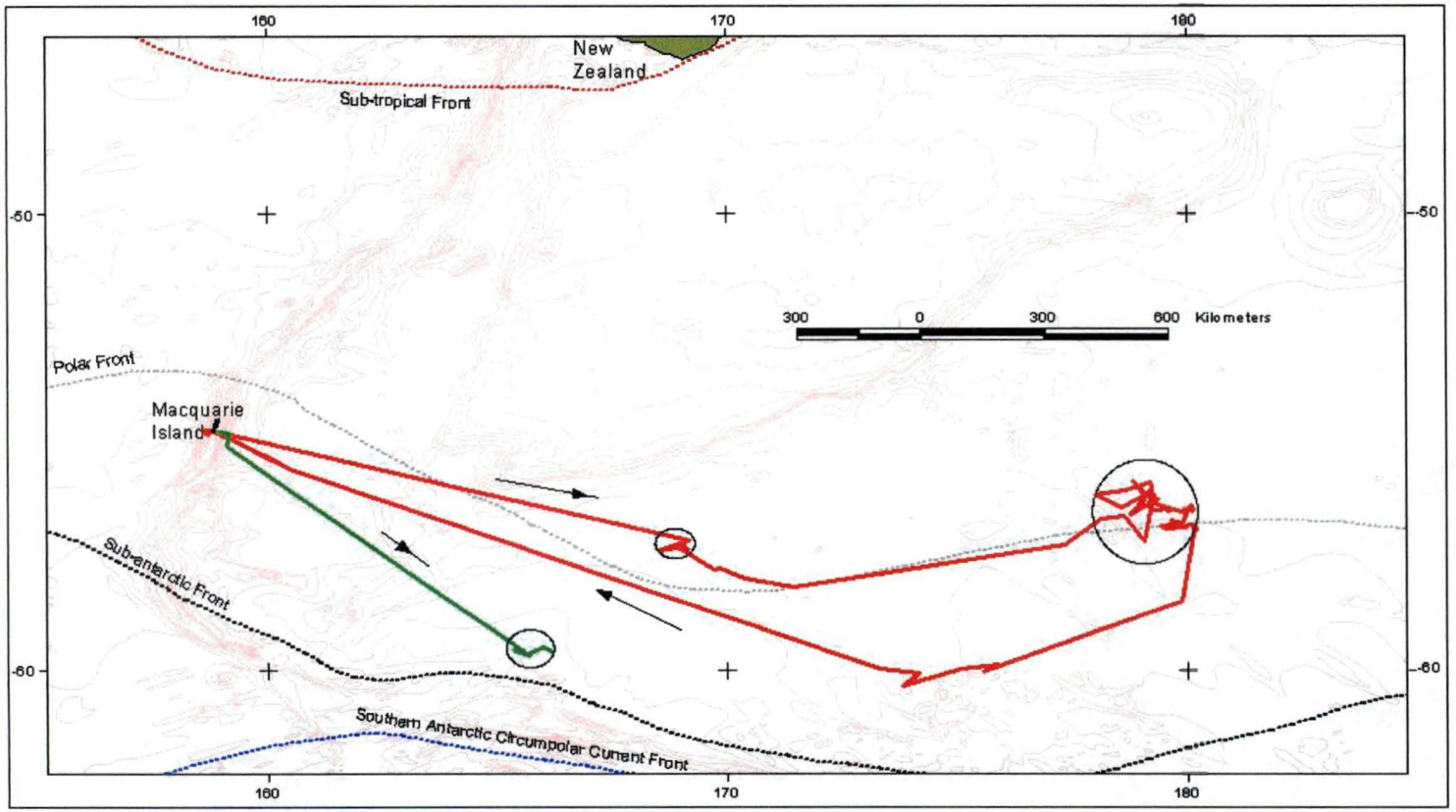
Legend

1st foraging trip
2nd foraging trip
200m Bathymetry contours
foraging areas

Appendix 7.9
Foraging track of male Grey-headed albatross in December 1999 and January 2000.
PTT_ID – GH_877_99



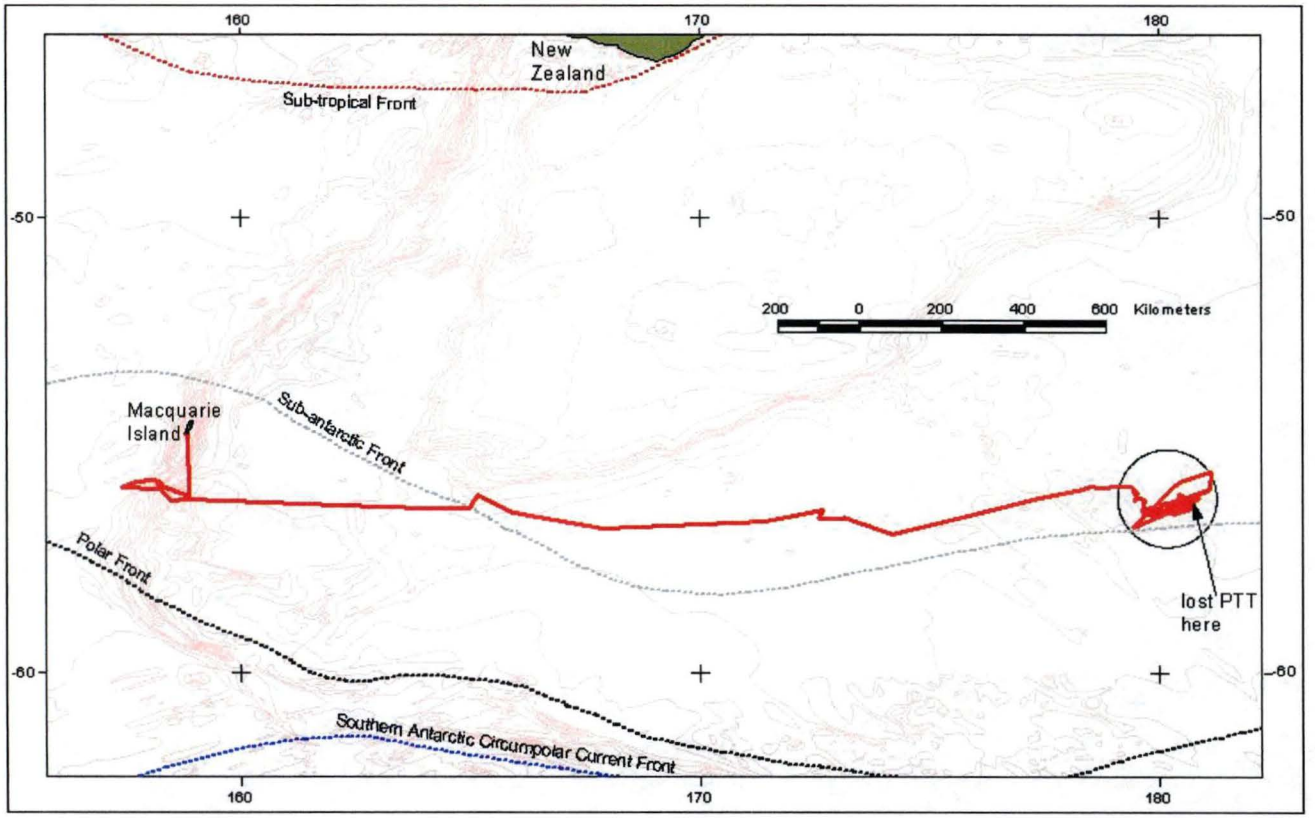
Appendix 7.10
Foraging track of female Grey-headed albatross in November and December 2000.
PTT_ID – GH_874_00



Legend

1st foraging trip
2nd foraging trip
200m Bathymetry contours
Foraging areas

Appendix 7.11
Foraging track of Grey-headed albatross in November and December 2000.
PTT_ID – GH_876_00



Legend

1st foraging trip — 200m Bathymetry contours — foraging area

Chapter 8 – Provisioning strategies of Light-mantled sooty albatrosses on Macquarie Island

8.1 INTRODUCTION

Light-mantled sooty albatrosses (*Phoebetria palpebrata*) have an estimated annual breeding population of 1000-1150 pairs on Macquarie Island (T. Disney –unpublished data cited in Gales 1998) and normally fledges a chick every two to three years when successful (Chapter 5). This population is thought to comprise 5-10% of the global breeding population and its IUCN status is listed as 'data deficient' (Croxall and Gales 1998). Like the other albatross and giant petrel species breeding on Macquarie Island, Light-mantled sooty albatrosses are also known to be caught and killed by long-liners fishing for tuna (Gales 1998) and the foraging areas identified by Weimerskirch and Robertson (1994) also suggest that this species is at risk from the expanding Patagonian Toothfish (*Dissostichus eleginoides*) fishery in Southern Ocean waters (Weimerskirch 1998).

Due to the paucity of biological data on this species in general, the relatively large population breeding on Macquarie Island and the potential risk associated with fisheries, several aspects of the ecology and biology of this species were investigated as part of the current study (Chapters 3,4,5,6). The provisioning regime of this species has not been previously documented in detail at any breeding location (in contrast to the other albatross species breeding on Macquarie Island) and therefore a study into this aspect was also initiated as part of the current study.

Although the growth of procellariiform chicks has been studied over several decades (Ricklefs 1968a; Ricklefs 1973; Ricketts and Prince 1981; Ricklefs 1983; Ricketts and Prince 1984) comprehensive analyses of provisioning regimes were not possible until the late 1980's and 1990's with the application of sophisticated automatic tracking systems and in some studies, automatic weighing platforms with artificial nest bowls (Prince and Walton 1984, Reid *et al.* 1999; Huin *et al.* 2000, Hedd *et al.* 2002). The use of remote tracking equipment with the automatic weighing nests (or frequent manual weighing) allows the contribution of each parent to be quantified and several studies have shown this aspect to be important in comprehensively describing the provisioning regime of a species (Chaurand and Weimerskirch 1994b; Weimerskirch *et al.* 1994a, Hedd *et al.* 2002).

Of particular importance in this context is the regulation of foraging trips during chick rearing. Most pelagic Procellariiformes studied during this period of the breeding cycle utilise

a combination of long trips into pelagic waters and short trips over more neritic waters closer to land. Some species alternate long and short foraging trips (e.g. Blue petrels *Halobaena caerulea* and Thin Billed Prions *Pachyptila belcheri*) while others have been shown to make repeated cycles of several short trips followed by a long trip (e.g. Wandering albatrosses *Diomedea exulans*, Yellow-nosed albatross *Thalassarche carteris*, Antarctic Prions *Pachyptila desolata* and White chinned petrels *Porcelain aequinoctialis*) (Chaurand and Weimerskirch 1994b, Cherel *et al.* 2002a; Cherel *et al.* 2002b, Weimerskirch *et al.* 1994a; Weimerskirch *et al.* 1995; Weimerskirch *et al.* 1999; Catard *et al.* 2000). Some species, particularly those that tend to forage in neritic waters, do not utilise an alternating strategy, preferring to maintain a primarily neritic (e.g. Black-browed albatrosses (*Thalassarche melanophrys*), Campbell albatrosses (*Thalassarche impavida*), Shy albatrosses (*Thalassarche cauta*)) or primarily pelagic (e.g. Grey-headed albatrosses (*Thalassarche chrysostoma*)) foraging regime (Huin and Prince 2000; Hedd *et al.* 2002; Waugh *et al.* 2000)

Studies to date (see above) have shown that the decision to undertake a long or short foraging trip appears related to the compromise between maintaining adult body condition and fulfilling the nutritional requirements of the chick. Drent and Daan (1980) described this conundrum in detail and suggested that there was a 'threshold' body condition below which adults would not go in order to sustain a chick, and this has been demonstrated by manipulative experiments on several species of Procellariforme (e.g. Chaurand and Weimerskirch 1994a; Weimerskirch *et al.* 2000c). It has been shown in Procellariiformes that short trips increase the energy flow to the chick at the expense of the body condition of the parent, while longer trips allow the parent to increase mass and condition (Weimerskirch *et al.* 1994a). Light-mantled sooty albatrosses from Iles Kerguelen were tracked during the brooding period (Weimerskirch 1998) but foraging strategies of this species after the brood-guard are largely unknown.

Prior to this study, Light-mantled sooty albatrosses were one of the few widely distributed albatross species to yet have their provisioning regime described in detail. In addition to the paucity of data on the foraging regime of this species during provisioning, the growth rate of Light-mantled sooty albatross chicks has been described in detail by only a few studies (Weimerskirch *et al.* 1986; Thomas *et al.* 1983; Berruti 1979) and in all cases this aspect formed a small part of a much broader ecological study. The aim of the current study was to comprehensively quantify chick growth of this population and describe the foraging routine used during the provisioning regime on Macquarie Island, particularly in the context of strategies utilised by other populations and species around the world.

8.1.2 Summary of research questions

1. What are the provisioning patterns (e.g. feeding frequencies, fasting lengths and meal sizes) of Light-mantled sooty albatross chicks on Macquarie Island ?

2. What are the growth rate parameters of Light-mantled sooty albatross chicks and can it be adequately described using previously described growth curves ?

3. How do provisioning parameters and growth rates vary with the age of the chick ?

4. How do these parameters compare with that found for other species with similar life-history attributes ?

8.2 DATA PROCESSING AND ANALYSES

Full details of the field testing and installation of the automatic weighing nests are contained in Chapter 2, Sec 2.2.6.

8.2.1 Downloading

After the automatic weighing nests were deployed, weights were recorded by the dataloggers every 10 minutes. These data were downloaded every 3-10 days from the dataloggers in situ, using a PC laptop without disturbing the chick. These data were than converted to kilograms (±10g) using previously calculated calibration constants and stored in spreadsheets. A main spreadsheet containing times and weights was created for each nest and data were added to these spreadsheets within a day of being downloaded.

Data were downloaded from the Automatic Tracking System (ATS) datalogger every 5-14 days and in a similar manner to the nest data were added to a main spreadsheet containing the details of each transmitter.

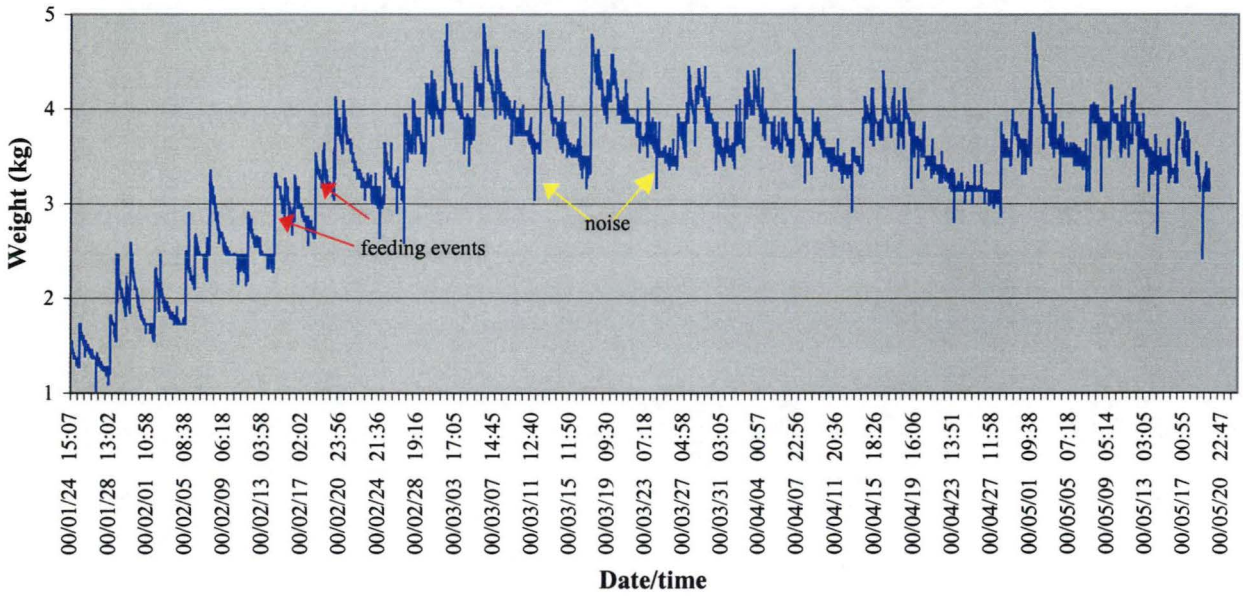
8.2.2 Processing and analyses

Feeding times and the weight of the food delivered were extracted manually from the auto-nest spreadsheets, and arrival and departure times were extracted from the ATS data. These data were then combined to calculate how much food each parent delivered during each visit. The ATS data were also used to investigate the attendance patterns during the provisioning regime. Feeding events rarely exceeded ten minutes and only those that appeared to exceed 20

minutes were split up into multiple feeding events. All feeding events could be attributed to a specific bird. If the transmitter on one of a pair failed then any feeding event that was not associated with the working transmitter was automatically assigned to the partner. The feeding frequency of each adult was then calculated, as was the duration of chick fasting.

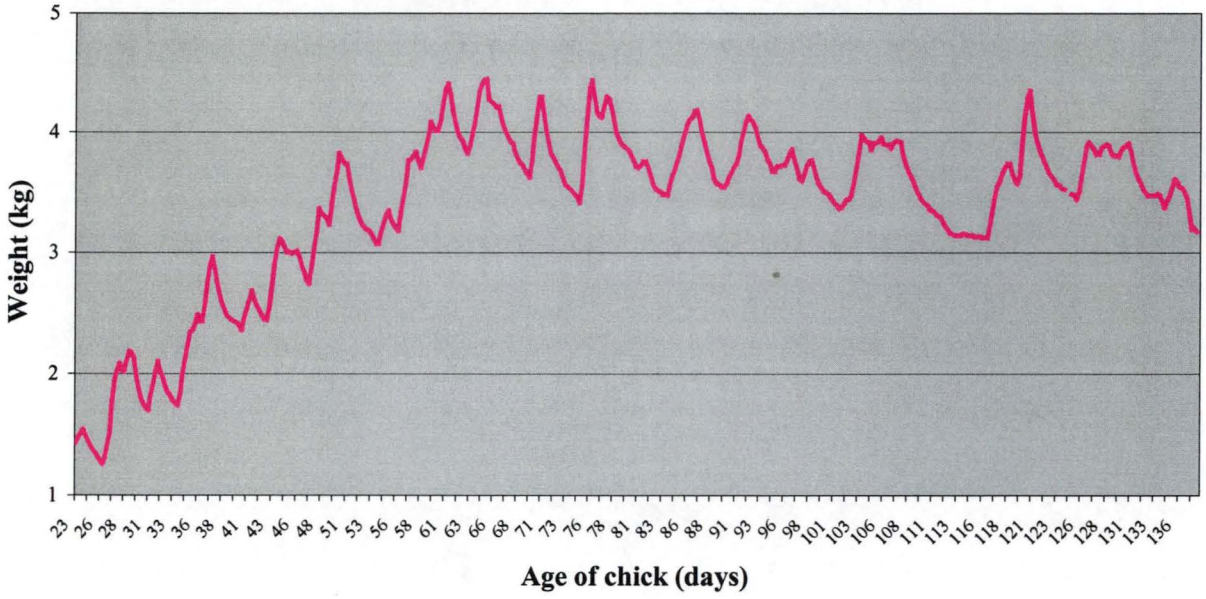
There were over sixteen thousand readings in the raw weight data from deployment to fledging for each nest (Figure 8.1). These data were simplified for the purposes of examining chick growth rates. A running 24-hour average was applied and four values per day were then extracted (00:00, 06:00, 12:00 and 18:00 – following Huin and Prince 2000). This reduced the number of data points to a more manageable 350-500 values (Figure 8.2).

Figure 8.1
Weight data from Light-mantled sooty albatross chick on nest 1_99 from deployment on 24/1/00 to fledging on 19/5/00 (10 minute intervals, 16 674 readings)



This smoothing procedure also filtered out most of the 'noise' that was present in the raw weight data. To test the validity of the simplification procedure, growth rates and curves were calculated from both the raw weight data and the simplified data and in both cases the same results were produced. Dates were also converted to the age of the chick for the growth rate analyses (Figure 8.2).

Figure 8.2
Simplified weight data of Light-mantled sooty albatross chick from nest 1_99, deployment (age-23 days) to fledging (age -139 days) (458 values)



Provisioning rates were examined over two temporal scales; firstly the mean growth rates over ten day periods were calculated and secondly growth rates were examined in the period up to the attainment of peak weight (1999/00 and 2000/01) and also during the period after peak weight to fledging (1999/00 only). Standard equations from the Richards' family of curves (Logistic, von Bertalanffy, Gompertz) were fitted to the simplified data (Richards 1959; Ricklefs 1968a; Brown and Rothery 1993) as was the growth equation created by Huin and Prince (2000). The form of these equations is contained in Appendix 8.1. The growth curve with the best fit (highest r^2) was used to estimate growth parameters for each chick.

8.3 RESULTS

Automatic weighing nests were installed under five chicks at the slopes north of Hurd Point in January 2000. These chicks were all aged between 22 and 28 days old and nests were left in place until each chick fledged in May or June 2000. There was no discernable effect of the nests on the chicks or the provisioning behaviour of the parents and all chicks fledged successfully (Section 8.3.1). One nest in 1999/00 developed a fault in the lead between the nest and the datalogger four weeks after it was installed. Consequently, only limited analyses could be conducted on data from these nests. In 2000/01 the nests were installed approximately five kilometres to the west of the original study site, on the slopes of Windsor Bay. These chicks were aged between 25 and 31 days old and the automatic weighing nests were removed after approximately two months when the chicks were aged between 85 and 90

days old. Again the nests did not appear to have any discernable impact on the provisioning behaviour of the parents and nest checks after our departure from Macquarie Island confirmed that all chicks fledged successfully.

8.3.1 Impact of the automatic weighing nests on provisioning regimes

The provisioning regimes of breeding birds with chicks on automatic weighing nests and control breeders with transmitters were compared. The feeding frequency (mean number visits per day) of each bird in the first 60 days after the brood-guard stage was calculated and used as the basis of these analyses. There were no significant differences in the feeding frequency of breeders with and without chicks on automatic weighing nests in 1999/00 (Mann-Whitney U, $Z = -1.2$, $p=0.242$, ns). In addition, the control chick fledged at 138 days of age in this season, which was very similar to the mean age of chicks on automatic weighing nests (140 ± 1.2 days). Due to transmitter failure only one breeding bird was used as a control in 2000/01; however, the feeding frequency of this bird was very similar to the mean feeding frequency of the breeders with chicks on automatic weighing nests (0.43 visits/day cf 0.42 ± 0.1 (s.e) visits/day).

8.3.2.Attendance patterns during provisioning

Breeders typically provisioned chicks in a cyclic attendance pattern comprised of a long foraging trip (5-23 days) followed by several short foraging trips (0.2 – 2.5 days), before undertaking another long foraging trip to begin the cycle again. The attendance provisioning data are summarised in Table 8.1 and clearly these long and short trips characterised the provisioning regime. The bi-modal distribution (Figure 8.3) also emphasises the predominance of long and short trips, with medium length trips being less common. These medium length trips often occurred successively, suggesting that they were utilised as a compromise between the longer and shorter trips. Very similar pattern of attendance during provisioning were observed in the two years of the study at the different locations. The ratio of long : medium : short trips was relatively consistent between birds (~6:1:3) and there were few deviations from the typical pattern.

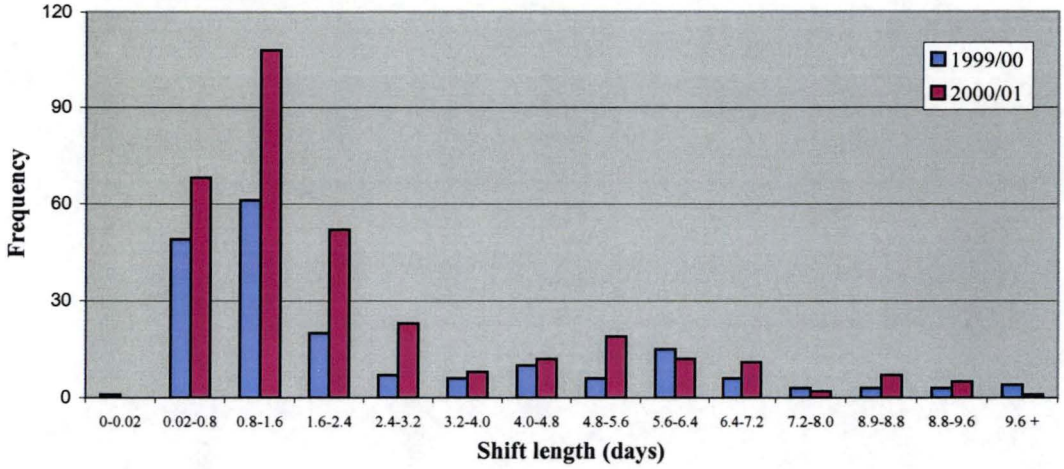
Table 8.1
Summary of attendance patterns of breeding Light-mantled sooty albatross whilst provisioning chicks on automatic weighing nests

Nest / bird	number of trips			mean duration (days)			mean overall (days)
	short	medium	long	short	medium	long	
1999/00 (Slopes north of Hurd Point) [A]							
n1_b1	16	6	10	1.1	3.4	7.2	3.9
n1_b2	12	5	8	1.5	4.0	7.3	3.4
n2_b1	21	4	7	1.2	3.1	8.0	2.9
n2_b2	37	5	9	1.1	2.9	5.9	2.1
n2_b1	33	9	8	0.9	3.1	5.2	2.0
n2_b2	41	5	10	1.2	3.7	6.1	2.3
n4_b1	22	8	7	1.2	3.1	6.8	2.7
n4_b2	44	3	8	0.9	3.3	7.3	1.9
n5_b1	28	4	11	1.1	3.5	6.7	2.8
n5_b2	19	6	8	1.1	3.5	9.5	3.6
all_99-00	228	38	70	1.1	3.3	7.5	2.6
2000/01 (Windsor Bay) [B]							
n1_b1	13	0	6	1.1	-	7.4	3.1
n1_b2	22	0	4	0.9	-	7.1	1.9
n2_b1	11	3	3	0.6	4.0	7.3	2.4
n2_b2	22	0	5	0.9	-	7.1	2.1
n3_b1	10	4	5	1.1	3.1	6.8	3.1
n3_b2	11	3	4	1.3	3.2	7.2	2.9
n4_b1	9	5	4	1.2	3.7	6.3	3.0
n4_b2	10	1	6	1.0	4.0	6.9	3.2
n5_b1	18	1	4	1.0	4.1	7.1	2.2
n5_b2	7	3	4	1.2	4.1	9.0	4.1
all_00-01	133	20	45	1.0	3.6	7.2	2.7

[A] - Deloyment period in 1999/00 - 24/1/00 - 31/5/00

[B] - Deployment period in 2000/01 - 23/1/01 - 28/3/01

Figure 8.3
Frequency of foraging trips of Light-mantled sooty albatrosses provisioning chicks on automatic weighing nests in 1999/00 (slopes north of Hurd Point) and 2000/01 (Windsor Bay)



8.3.3 Overall chick provisioning

Due to the different deployment durations in 1999/00 and 2000/01, analyses of chick provisioning in each year were generally conducted separately. To facilitate comparisons between the two years (and sites) the parameters were also calculated to Day 89 (the maximum deployment period in 2000/01) from the 1999/00 data. Deployment details and overall provisioning parameters are summarised in Table 8.2.

8.3.3.1 Entire provisioning period (1999-00)

Chicks were fed between 30 and 42 kilograms of food during the entire provisioning period (mean = 37.5 ± 2.3 kg) for an overall increase in body mass of 2-3 kilograms. The overall feeding frequency was relatively consistent between nests and chicks were fed on average every 1.4 to 1.9 days (mean = 1.6 ± 0.1 s.e days). In 1999/00 one pair fed its chicks much less frequently than the other three pairs (N1-3). However, this chick fledged at a similar age and mass to the other chicks, suggesting that there is some latitude in the frequency at which chicks need to be fed in order to fledge successfully. Further evidence for this was observed in 2000/01. Due to the small sample size and no unsuccessful chicks it was not possible to identify the upper and lower limits of feeding frequencies required to ensure that a chick fledged successfully. Mean meal size was even more similar across the nests averaging 520 ± 10g (range 510 – 540g).

Table 8.2

Summary of overall provisioning from automatic weighing nest deployment data, 1999/00 and 2000/01 [A]

Nest	Age installed (days)	Age removed (days) [B]	Duration (days)	# visits	Feeding frequency (visits/day)	Total amount food (kg)	Mean feed (kg)	Mean fast time days)	Overall provisioning rate (g/day)	Weight at fledging (kg)
1999/00 (slopes north of Hurd Point, nests in place until fledging)										
N1-3	25.6	141.7	116.0	61	0.53	30.82	0.51	1.9	265.6	3.1
N2-1	22.6	135.5	112.9	76	0.67	38.72	0.51	1.4	343.0	3.3
N4-7	24.5	137.7	113.2	76	0.67	39.14	0.52	1.4	345.7	2.8
N5-9	19.5	142.5	123.0	76	0.62	41.22	0.54	1.6	335.2	3.2
mean	23.1	139.4	116.3	72.3	0.62	37.5	0.52	1.6	322.4	3.1
s. e	1.3	1.7	2.3	3.8	0.03	2.30	0.01	0.1	19.1	0.2
1999/00 (slopes north of Hurd Point, *to day 89 to allow comparisons with 2000/01*)										
N1-3	25.6	*89*	63.4	39	0.62	20.80	0.53	1.8	328.2	-
N2-1	22.6	*89*	66.4	51	0.77	26.70	0.51	1.3	402.3	-
N4-7	24.5	*89*	64.5	51	0.79	27.58	0.54	1.3	427.5	-
N5-9	19.5	*89*	69.5	50	0.72	25.70	0.51	1.4	370.0	-
mean	23.1	-	65.9	47.8	0.72	25.20	0.52	1.4	382.0	
s. e	1.3	-	0.8	1.2	0.04	1.50	0.01	0.13	21.4	
2000/01 (Windsor Bay, nests in place until chicks 85-90 days old)										
N1-453	28.5	87.5	59.0	47	0.80	24.14	0.51	1.3	409.4	
N2-460	26.6	85.5	59.0	46	0.78	18.12	0.39	1.2	307.3	
N3-291	27.5	85.5	58.1	39	0.67	20.61	0.53	1.5	355.1	
N4-A277	24.6	84.6	59.9	37	0.62	21.75	0.59	1.5	363.1	
N5-285	25.6	85.6	59.9	39	0.65	21.44	0.55	1.5	357.7	
mean	26.6	85.7	59.2	41.6	0.70	21.20	0.51	1.5	358.5	
s. e.	0.7	0.5	0.3	2.0	0.04	1.0	0.03	0.06	16.2	
Provisioning to day 89 t-test			t (df=7)		0.40		0.22	0.20	0.89	
99/00 v 00/01			p-value		0.70		0.83	0.85	0.40	

[A] Nest 3/99 omitted due to faulty connection between nest and logger

[B] Equivalent to age at fledging in 1999/00

8.3.3.2 Provisioning to Day 89 (age of chick)

Similar provisioning parameters were observed in both the entire provisioning period and to Day-89. It appeared that chicks were provisioned more frequently to Day-89 relative to the entire provisioning but these differences were not statistically significant (One-way ANOVA, $F_{feed\_freq,2} = 2.1$, $p=0.17$). No significant differences in any of the other provisioning parameters were observed between the overall period and to day 89 (One-way ANOVA's: $F_{mean\_feed,2} = 0.04$, $p=0.96$; $F_{mean\_fast,2} = 0.77$, $p=0.49$; $F_{prov\_rate,2} = 2.4$, $p=0.14$). These tests also suggested that there were no significant differences between the Day-89 provisioning parameters from each year (and site).

8.3.4 Temporal variation in provisioning parameters

The temporal variation in the amount of food provided and the feeding frequency of chicks was examined by partitioning the deployment time (i.e. the age of the chick) into ten-day periods. The provisioning parameters in each of these periods were then calculated for each chick. The first and last ten-day periods were excluded from these analyses because there was often incomplete data from all nests for the entirety of these time periods.

8.3.4.1 Mean meal size

Mean meal size was one of the most consistent provisioning parameters of Table 8.1 with few differences observed between nests and between years. There was similar consistency in the ten-day temporal variation with mean meal size ranging from 470g to 550g for the entire provisioning regime (Figure 8.4). There was no evidence in any age related trend in the mean sizes delivered to chicks. However, there was considerable variation in the individual meal sizes delivered and single meals ranged in weight from 80g to 1030g. This variation was largely attributable to the cyclic pattern of long and short shifts identified in Section 8.3.3 and correlation analyses showed that the weight of each meal was significantly correlated with the length of time for which the bird had been foraging (Pearson $r_{193} = 0.55$, $p<0.001$).

8.3.4.2 Chick fasting intervals.

The mean fasting intervals in each ten-day period of chick provisioning are summarised in Figure 8.5. This figure illustrates how the interval between feeding events tended to increase as the chick grew older (both seasons) and Pearson Correlations indicated that the age of the chick was significantly correlated with mean fasting interval ($r_{15} = 0.64$, $p < 0.001$).

Figure 8.4
Mean meal size (± s.e) delivered to Light-mantled sooty albatross chicks in 1999/00 (Slopes north of Hurd point-4 nests) and 2000/02 (Windsor Bay - 5 nests)

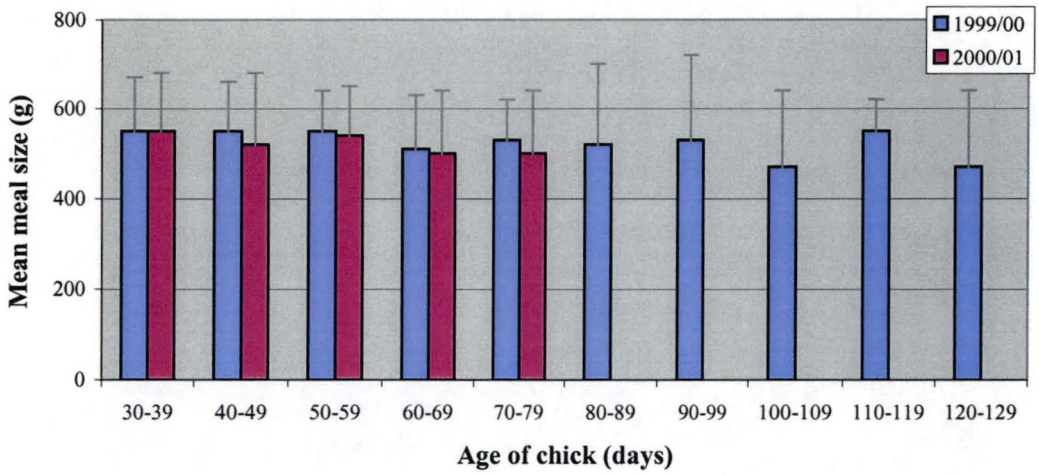
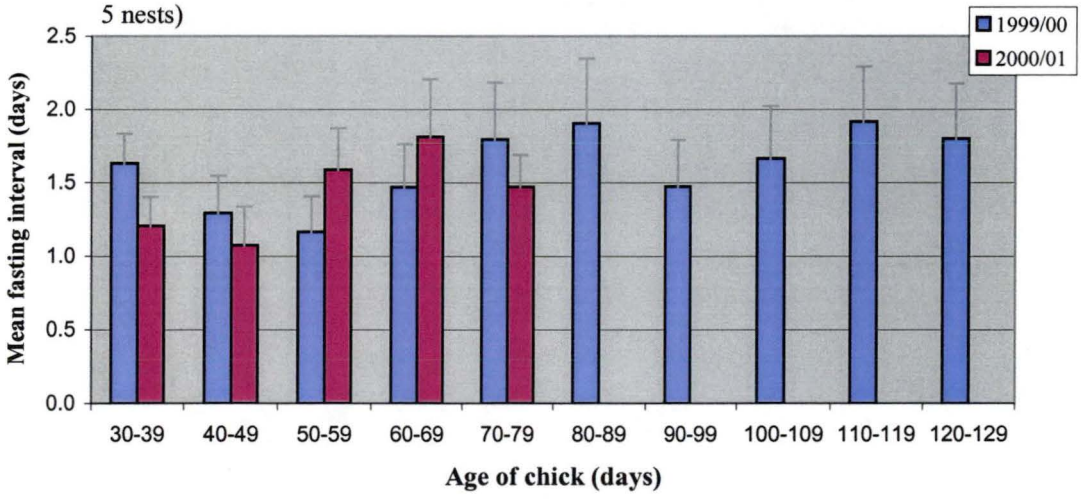


Figure 8.5
Average time between successive meals delivered to Light-mantled sooty albatross chicks in 1999/00 (slopes north of Hurd Point - 4 nests) and 2000/01 (Windsor Bay - 5 nests)



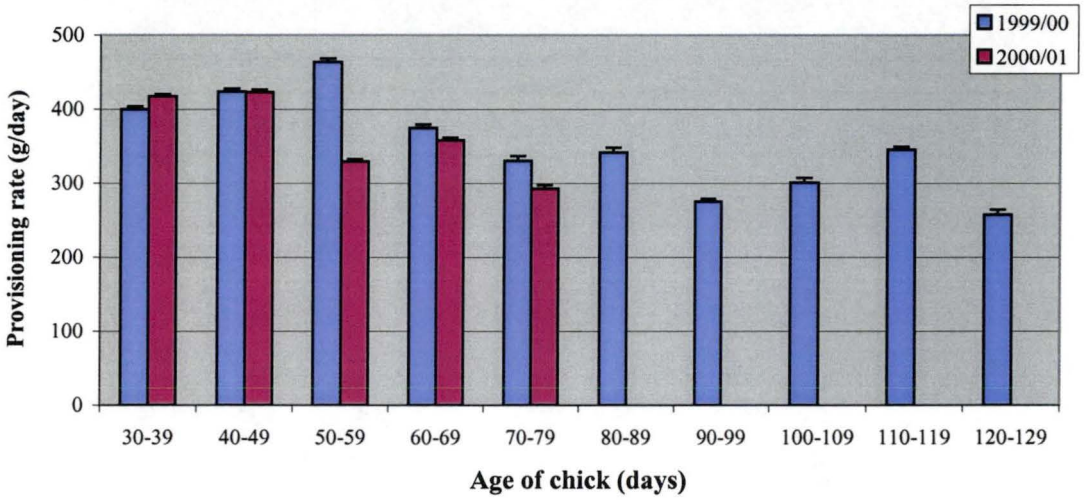
This increase was relatively gradual and not consistent throughout the provisioning regime. There was some indication of a somewhat bi-modal distribution (1999/00), with chicks fed more frequently between the age of 90-110 days than the preceding and following age intervals (Figure 8.5). Fasting intervals were extremely variable with chicks occasionally receiving successive meals within hours of each other, or at the other extreme, fasting for up to ten days when both parents were on long foraging trips.

Chicks were fed most frequently between the ages of 40 and 60 days (1999/00) and 30 and 50 days (2000/01). The fast interval also increased more rapidly in the first 60 days of nest installation during 2000/01; however, comparisons of the mean values showed that there were no significant differences between the two years (Paired-t test, $t_4 = 0.22$, p=0.8).

8.3.4.3 Chick provisioning rate

As mean meal size was similar throughout the provisioning regime (Section 8.3.4.2) and feeding frequency declined, the overall provisioning rate declined with age (Figure 8.6).

Figure 8.6
Mean provisioning rate (± s.e) of Light-mantled sooty albatross chicks, in 1999/00 (slopes north of Hurd Point - 4 nests) and 2000/01 (Windsor Bay - 5 nests)

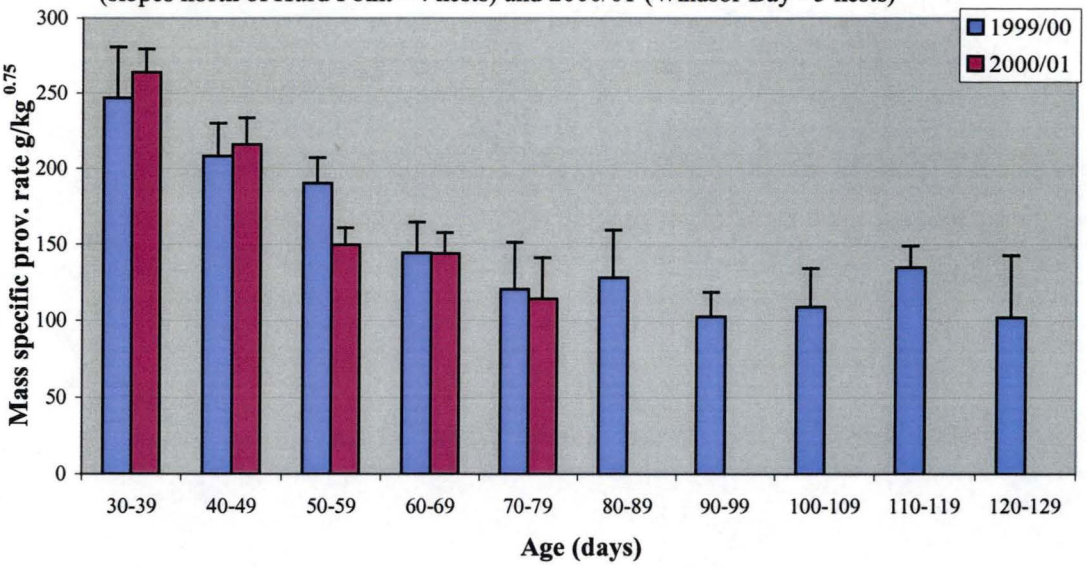


Statistical tests also showed a significant negative correlation between provisioning rate and the age of the chick (Pearson $r_{15} = -0.78$, $p < 0.001$). A similar correlation was also observed between the provisioning rates and the concurrent mean fasting intervals (Pearson $r_{15} = -0.62$, p=0.007). Mean provisioning rates were similar at the two locations in the first 60 days of nest deployment and there was no statistical evidence to suggest the differences observed between the two sites were significant (paired-t, $t_4 = 1.3$, p=0.3). There was no relationship between provisioning rate and the final fledging weight of the chick (r_4=-0.1, p=0.47).

8.3.4.4 Mass-specific provisioning rate

To assess if the chicks mass influenced the provisioning rate, mass specific provisioning rates were calculated in $g.kg^{0.75}$ and are summarised in Figure 8.7.

Figure 8.7
Mass-specific provisioning rate of Light-mantled sooty albatross chicks in 1999/00 (slopes north of Hurd Point - 4 nests) and 2000/01 (Windsor Bay - 5 nests)



The mass-specific provisioning rate decreased sharply between the ages of 20 and 80 days (both years), which is also the period of the most rapid chick growth. Mass-specific provisioning plateaued at just over 100 $g.kg^{-0.75}$ post-80 days of age, and remained at this level until the chick fledged (1999/00 only).

8.3.5 Contribution of each parent

The use of the ATS system allowed the contribution of each parent to be quantified. These data are summarised in Table 8.3 and show that in general the provisioning load was shared equally between birds of a pair. The proportion of visits each parent made was strongly correlated with the proportion of the total food provided by that bird (Pearson r_5= 0.87, $p<0.01$), indicating that those birds who made more frequent trips did not do so at the expense of food mass (and vice versa).

Although there was variation in some of the provisioning parameters between birds of a pair, paired t-tests provided no evidence to suggest that these differences were statistically significant (df=8 : t_{total} = -0.09, p=0.9; t_{visits} = -0.8, p=0.4; t_{mean} = 0.5, p=0.6; t_{rate} = 0.3, p=0.7 all ns). The largest difference between birds of a pair was observed on N2-99 in 1999/00 where Bird 2 made 50 % more feeding visits and delivered 45 % more food than Bird 1.This is largely attributable to Bird 1 undertaking very few short foraging trips and there was some evidence that Bird 2 increased the frequency of its trips to compensate (see also Table 8.1).

Table 8.3
Contribution of each parent to provisioning regime of chicks on automatic weighing nests in 1999/00 (24/1/00 - 31/5/00) and 2000/01 (23/1/01 - 28/3/01)

	Bird 1				Bird 2			
Nest ID	**Total food (kg)**	**# visits**	**Mean feed (kg)**	**Rate (visits /day)**	**Total food (kg)**	**# visits**	**Mean feed (kg)**	**Rate (visits /day)**
1999/00 (slopes north of Hurd Point, nests in place until fledging)								
N1-3	15.8	34	0.46	0.29	15.0	27	0.56	0.23
N2-1	15.9	30	0.53	0.27	22.9	46	0.50	0.41
N4-7	19.7	33	0.60	0.29	19.5	43	0.45	0.38
N5-9	23.3	40	0.58	0.33	17.9	36	0.50	0.29
2000/01 (Windsor Bay, nests in place until chicks 85-90 days old)								
N1-453	10.6	20	0.53	0.34	13.6	27	0.50	0.46
N2-460	7.1	18	0.39	0.31	11.1	28	0.40	0.47
N3-291	10.0	20	0.50	0.34	10.6	19	0.56	0.33
N4-A277	12.3	19	0.64	0.32	9.5	18	0.53	0.30
N5-285	12.9	24	0.54	0.40	8.5	15	0.57	0.25

8.3.5 Chick growth

The mean weight of the chicks when the nests were installed was 1.4 ± 0.1 (se) kg (n = 10). Due to the limited nest deployment time in 2000/01 and the malfunction of one nest in 1999/00, weight data from deployment to fledging were only obtained for four chicks. The mean final fledging weight of these chicks was 3.1 ± 0.1 kg and they were fed on average 37.5 ± 2.3 kg from installation to fledging. These chicks reached peak mass (4.8 ± 0.2 kg) at 79 ± 8.8 days but this was extremely variable and ranged from 63 to 102 days. The weight of most chicks began to plateau after 50-70 days (Figures 8.8a,b) and the variation in the age at which peak weight was attained is more attributable to weight spikes caused by large or successive feeds over short periods of time. Chicks were fed less frequently as they grew closer to fledging, however, parents still attended the nest until the chicks had fledged. Composite growth curves using pooled nest data from each year and the entire pooled data set illustrate the similarities of the weight gain by chicks at the two sites during the relatively the first 60-70 days of the provisioning regime (Figure 8.8a and 8.8b).

Figure 8.8a
Composite growth curves of Light-mantled sooty albatross chicks in 1999/00 (24/1/00-31/5/00 -slopes North of Hurd Point - 4 nests) and 2000/01 (23/1/01 - 28/3/01 - Windsor Bay - 5 nests)

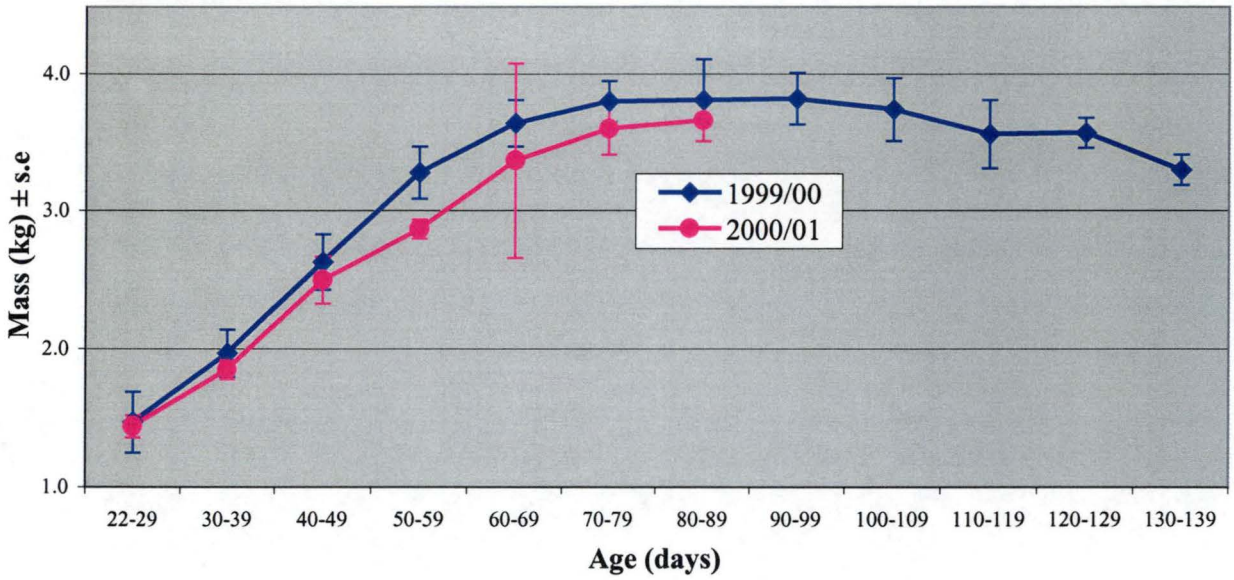
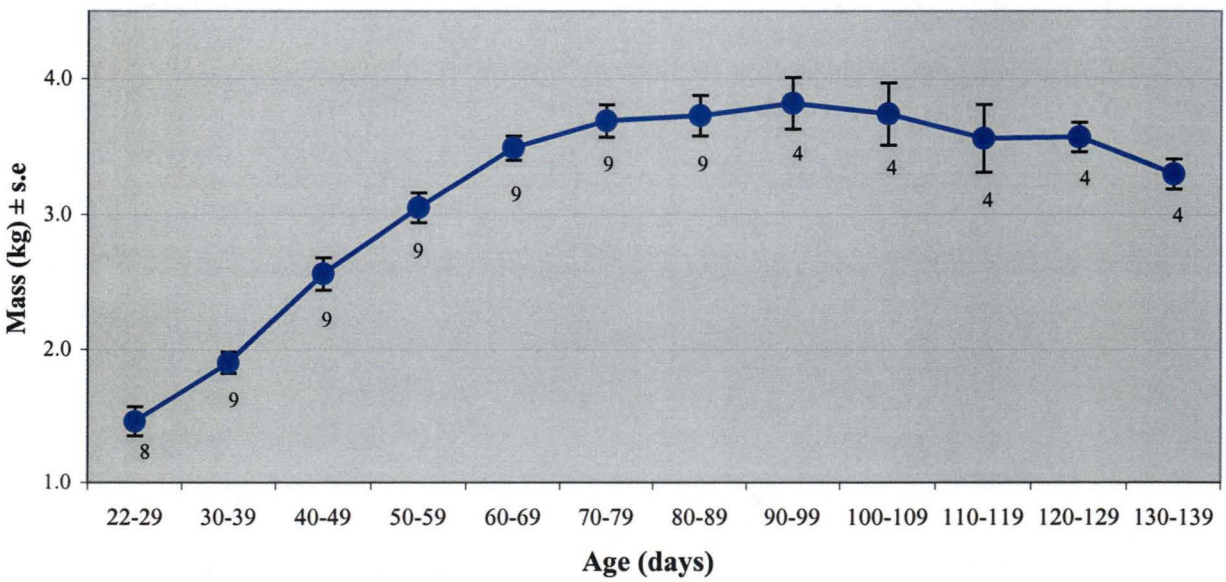


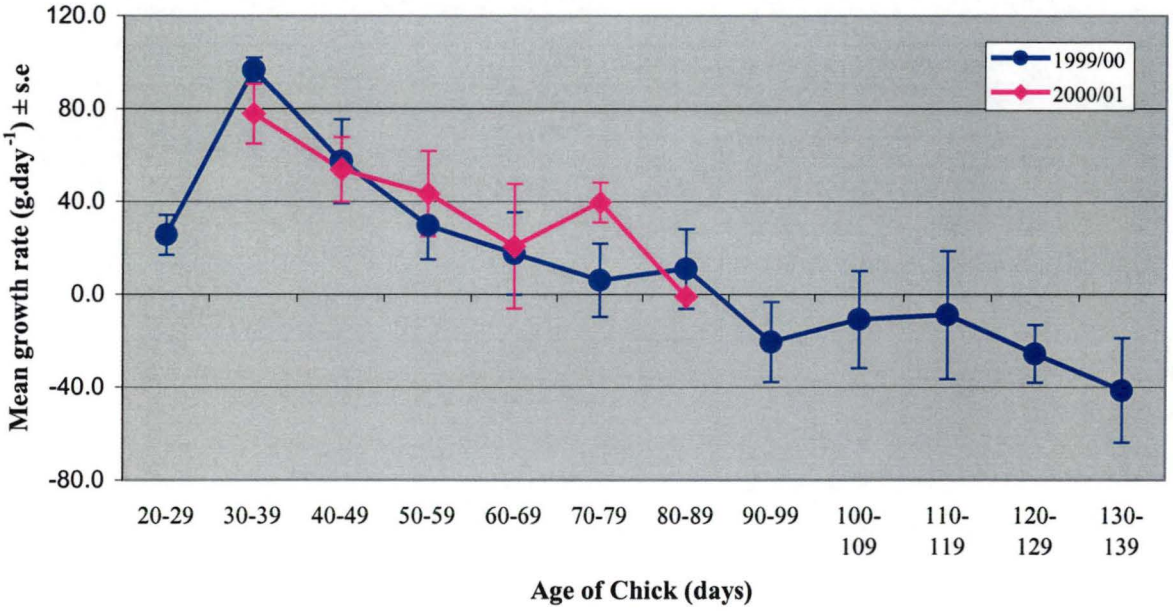
Figure 8.8b
Composite growth curves showing weight gain of Light-mantled sooty albatross chicks on Macquarie island (pooled data from 1999/00 and 2000/01 - sample sizes shown on points)



8.3.5.1 Temporal variation in growth rates

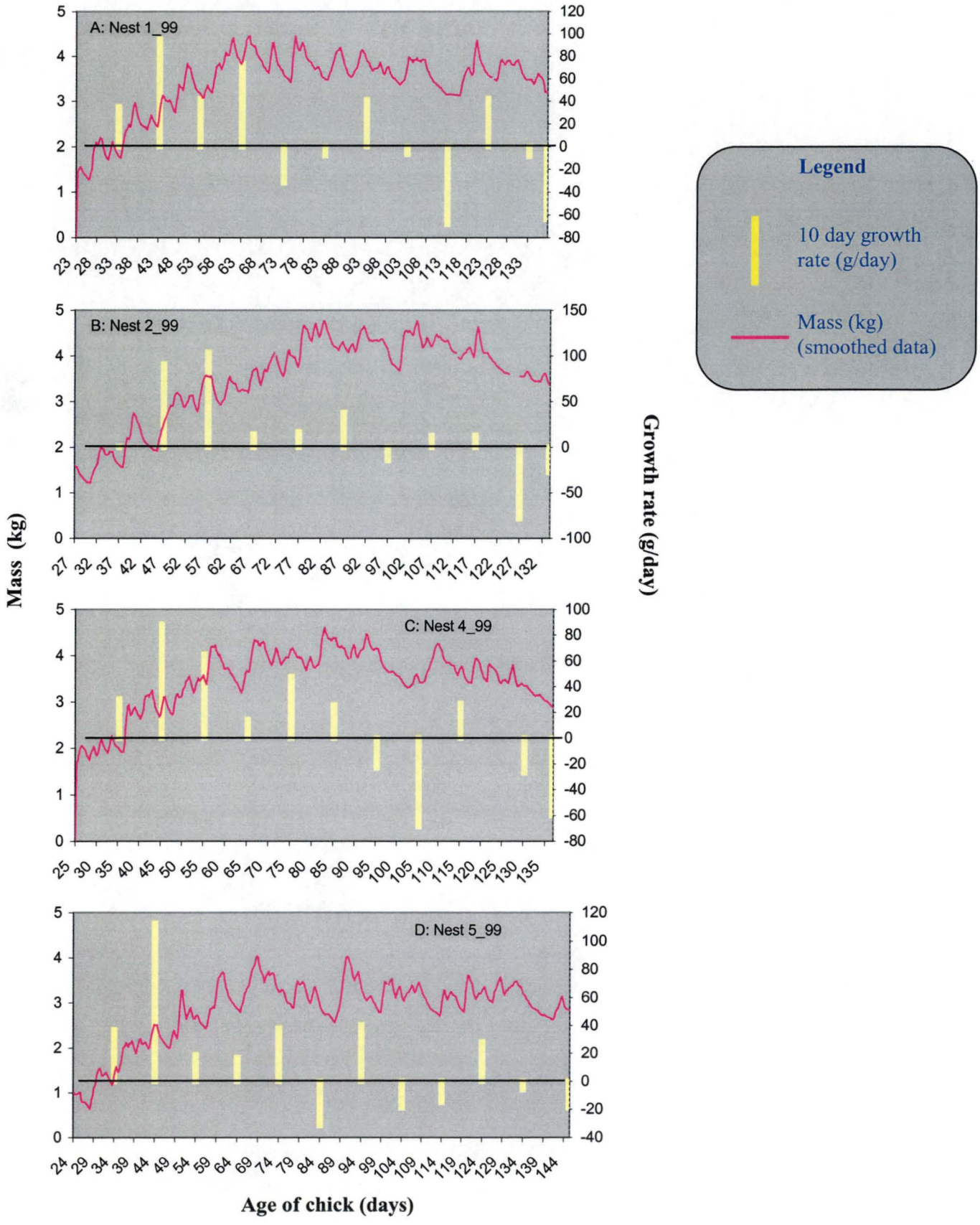
The mean growth rates in each 10-day period were calculated for each year (Figure 8.9) and although there was some variation, the trend is similar and the differences were not statistically significant (paired t, $t_5 = -0.4$, $p=0.8$).

Figure 8.9
Mean growth rates of Light-mantled sooty albatross chicks in 1999/00 (24/1/00- 31/5/00 -slopes North of Hurd Point - 4 nests) and 2000/01 (23/1/01 - 28/3/01 - Windsor Bay - 5 nests)



The large standard errors in Figure 8.9 illustrate the variation in growth rates between chicks. To examine this individual variation in more detail, growth rates for each chick in each ten-day period were calculated and are shown in Figures 8.10a-d in conjunction with the smoothed weight data from 1999/00 (24-hour running average and four times extracted). These figures show that growth rates were generally positive and high when the chick was between 40 and 60 days of age, following which they decreased and often became negative as the weight of the chick began to plateau and gradually decline. A similar pattern was also observed in the growth rates in the 2000/01 season; however, due to the reduced time that the nests were in place, most growth rates recorded were positive (see Appendix 8.2a-e for similar graphs) and it is likely that the peak weight may not have been reached in some of these nests.

Figure 8.10
Weight increase of individual Light-mantled sooty albatross chicks (1999/00 -smoothed weight data) from nest deployment (24/1/00) to fledging (31/5/00) with concurrent ten-day growth rates



The above trends in growth rates were consistent with the reduction in feeding frequency observed in the latter half of the provisioning regime and although the mean rates during the weight recession period are consistent, Figures 8.3a-d indicates that growth rates throughout this time period were extremely variable. The overall mean growth rate in the ten-day periods prior the attainment of peak mass was 47.8 ± 7.3 (s.e) $g.day^{-1}$ (n=21); post peak mass this rate was –15.09 ± 7.1 $g.day^{-1}$ (n=25) and the mean overall growth rate for all ten-day periods was 13.6 ± 6.9 $g.day^{-1}$ (n=46).

8.3.5.2 Fitting growth curves

Growth curves were fitted to both complete (1999-00 only, five nests from deployment to fledging-e.g. see Figure 8.8b) and incomplete chick growth datasets (all nests, deployment to age 85 days – Figure 8.8a). Growth to Day-85 was used as all nests were deployed for this period and all but one chick in 1999/00 had obtained peak weight by this age. The peak weight before Day-85 was used for this chick when fitting curves (and was almost exactly the same as weight at 103 days). Using the data of Thomas et al. (1983), the weight at hatching was estimated to be 180g and this value was used when fitting all growth curves. Gompertz growth curves had the best fit (cf Logistic, non Bertalanffy, and double-Gompertz-see Appendix 8.1) to both types of data and the parameters calculated from these equations are shown in Table 8.3 (1999/00 only - whole data sets) and Table 8.4 (both years - growth to Day 85). The Gompertz curves fitted the 'growth to Day-85' data better than the 'all data' curves; and the parameters estimated using the former curves were closer to the observed values.

The mean predicted asymptotic weight (calculated using the 'provisioning to Day-85' dataset) were very similar to the mean observed peak weight (4.7 ± 0.3 kg cf 4.4 ± 0.2 kg); whereas the asymptotic weight estimate obtained using the entire dataset was significantly lower than the observed value (3.7 ± 0.02 kg cf 4.6 ± 0.2 kg; t_8 = -3.8, p=0.005). Similarly the growth constants estimated by the using the 'growth to Day 85 dataset' were more similar to the observed values than those estimated using the entire dataset. The discrepancy between the parameter estimates in Table 8.3 and the observed values is likely to be attributable to the protracted and gradual mass recession period observed in most chicks in the latter half of the provisioning period. However, this protracted and gradual recession period is also likely to be a major factor in the fit of the Gompertz curve to these data (compared to the other curves fitted).

Table 8.4
Growth parameters obtained from observed data (black) and Gompertz curves (blue) for entire provisioning period Light-mantled sooty albatross chicks in 2000/01

Nest_ID	wt deploy (kg)	age deploy (days)	Asym. mass (A)	s.e	Peak wt (kg) (W_{max})	Age peak (days) (t_{max})	Growth rate to peak ($g.day^{-1}$) (k_p)	Growth constant k_1 (*1000)	s.e	Age max growth (days) (t_i)	s.e	Fledge (end) wt (W_{end})	Age fledge (days)	Overall growth rate ($g.day^{-1}$) (k_t)	Declining growth rate (k_d)	Gompertz r^2
N1_99	1.43	23.3	3.74	0.02	4.44	65.0	72.1	86.7	4.3	25.7	0.5	3.17	137.5	15.2	-17.5	0.81
N2_99	1.60	27.3	4.19	0.03	4.77	103.8	41.4	58.4	2.6	33.0	0.5	3.36	133.8	16.5	-47.0	0.87
N3_99	1.37	25.0	3.51	0.03	4.56	72.0	67.7	75.8	4.1	27.3	0.6	2.77	150.8	11.1	-22.7	0.80
N4_99	1.67	25.0	3.78	0.02	4.59	82.8	50.6	84.1	5.3	25.0	0.6	2.88	136.5	10.9	-31.8	0.73
N5_99	1.01	24.3	3.18	0.02	4.03	69.0	67.4	86.7	4.2	30.4	0.4	2.84	145.5	15.1	-15.5	0.82
mean ± s.e	1.42 ± 0.1	25.0 ± 0.9	3.68	0.02	4.59 ± 0.19	80.3 ± 8.8	60.4 ± 7.1	78.3	5.4	28.3	1.5	3.0 ± 0.1	140.8 ± 3.2	13.8 ± 1.2	-26.9 ± 5.8	-
All_99			3.64	0.01				77.9	2.4	27.8	0.3					0.69

Table 8.5
Growth parameters obtained from observed data (black) and Gompertz curves (blue) for the first 85 days of the provisioning regime of Light-mantled sooty albatross chicks in 1999/00 and 2000/01

Nest_ID	Wt deploy (kg)	Age deploy (days)	Asym. Mass (kg) (A)	s.e	Peak wt (kg) (W_{max})	Age peak (days) (t_{max})	Growth rate to peak ($g.day^{-1}$) (k_p)	growth constant k_1 (*1000)	s.e	Age max growth (days) (t_i)	s.e	Age 85 wt (kg) (W_{85})	Age at end (days)	Growth rate ($g.day^{-1}$) (k_{85})	Gompertz r^2
N1_99	1.43	23.3	6.86	0.88	4.44	65.0	72.1	27.7	4.2	39.4	4.9	3.82	85.0	38.7	0.83
N2_99	1.60	27.3	4.72	0.07	4.77	84.0	56.8	51.8	4.1	35.7	0.5	4.20	85.0	45.1	0.93
N3_99	1.37	25.0	3.74	0.17	4.56	72.0	67.7	58.5	7.5	27.2	0.83	3.01	85.0	27.3	0.81
N4_99	1.67	25.0	4.31	0.08	4.59	82.8	51.6	52.0	3.7	24.9	0.54	4.38	85.0	45.1	0.90
N5_99	1.01	24.3	4.20	0.26	4.03	69.0	67.4	45.9	5.1	34.8	1.48	2.77	85.0	29.0	0.90
N1_00	2.14	30.3	4.31	0.27	4.33	88.0	37.90	31.3	6.0	20.35	1.7	4.33	85.0	38.2	0.67
N2_00	1.35	28.3	4.76	0.33	4.26	69.8	70.10	33.1	4.5	36.97	2.1	3.39	85.0	35.6	0.83
N3_00	1.02	28.0	4.72	1.77	4.62	83.0	65.50	43.6	4.1	33.78	0.9	4.41	85.0	59.5	0.88
N4_00	1.17	26.3	5.48	0.95	4.02	68.0	68.30	26.6	5.9	38.71	6.8	3.19	85.0	34.4	0.86
N5_00	1.28	27.3	3.8	0.18	4.10	77.8	55.80	50.3	7.2	28.55	0.9	3.50	85.0	37.8	0.76
mean ± s.e	1.4 ± 0.2	26.5 ± 0.5	4.69	0.30	4.37 ± 0.16	75.9 ± 0.9	61.32 ± 1.03	42.1	1.1	32.04	0.8	3.70 ± 0.25		39.07 ± 0.96	-
All_chicks			4.69	0.77				36.6	1.4	31.7	4.3				0.81

Chicks were growing most quickly at approximately 30 days of age and this was the most similar parameter estimated by fitting growth curves to the two types of data. A general Gompertz growth curve was fitted to the pooled data from all chicks (to Day-85) to provide a general model of growth for this species (excluding the mass recession period). The r^2 value for this curve was high (0.81) suggesting a good fit to the data with chicks growing at 36.6 ± 1.4 g.day^{-1}, growing at their fastest rate at 31.7 ± 4.3 days of age and reaching an asymptotic mass of 4.69 ± 0.77 kg. An attempt was also made to fit separate curves (e.g. reverse Gompertz (Huin and Prince 2000), logistic, linear, exponential and polynomial) to the mass recession period; however, none of these curves fitted the data adequately (as indicated by low r^2). The lack of fit may be due to the variation caused by a periods of both episodic and frequent feeding events during the mass recession period.

8.3.5.3 Growth from t_{10} to t_{90}

Growth was also described as the time it took for chicks to grow from 10% (t_{10}) to 90% (t_{90}) of asymptotic mass (Table 8.5). The mean time to grow from t_{10} to t_{90} was 78 ± 7.2 day and there was no significant differences between years (t_8=1.1, p=0.3). The only parameter in these analyses that was different between years was the average daily mass gain (t_8=2.8, p=0.02) suggesting that there may actually have been differences in growth rates of the chicks at the two sites. The mean growth rate in 1999/00 at the slopes north of Hurd Point was higher (55.5±2.6 g.day^{-1}) than that observed in 2000/01 at Windsor Bay (49.9±2.7 g.day^{-1}); however, when examined as a percentage of asymptotic mass, growth rates were not significantly different between years (Table 8.5) and corresponded to an overall increase of 1.1±0.1 % of asymptotic mass per day.

8.3.5.4 Relationship between provisioning rate and growth parameters

The relationship between the predicted parameters shown in Table 8.5 and provisioning rate were examined using Pearson Correlation Tests. These tests showed that there was no relationship between overall provisioning rates and growth rates (r_9=0.2, p=0.3); however negative correlations were found between provisioning rate and the age at maximum growth (r_9=-0.7, p=0.016) and the asymptotic mass (r_9= -0.7, p=0.026). No relationship was found between provisioning rates and the mass at fledging (r_4=-0.1, p=0.47).

Table 8.6
Growth of Light-mantled sooty albatross chicks as expressed as the time taken to grow from 10% (t_{10}) to 90% (t_{90}) of asymptotic mass
Growth during this time is expresses as an absolute mass gain (g.day-1) and as a percentage of the asymtotic mass gained per day.

Nest/Id	Asymptotic mass (kg) [A]	Age (days)			Average daily mass gain	
		t_{10}	t_{90}	t_{10-90}	g	as % asymptotic mass
1999/00 (slopes north of Hurd Point)						
N1_99	6.86	9	121	111	49.3	0.7
N2_99	4.72	20	79	60	63.4	1.3
N3_99	3.74	13	66	53	56.7	1.5
N4_99	4.31	9	68	59	58.1	1.3
N5_99	4.2	17	84	67	50.0	1.2
mean	4.77	13	84	70	55.5	1.2
s.e	0.54	2	10	11	2.6	0.1
2000/01 (Windsor Bay)						
N1_00	4.31	6	92	86	40.1	0.9
N2_00	4.76	12	105	93	40.9	0.9
N3_00	4.72	15	85	71	53.4	1.1
N4_00	5.48	7	123	116	37.8	0.7
N5_00	3.8	12	73	61	49.6	1.3
mean	4.61	10	96	85	44.3	1.0
s.e	0.27	2	9	10	3.0	0.1
t (df=8)	*0.3*	*1.2*	*-0.9*	*-1.1*	*2.8*	*1.4*
p-value	*0.8*	*0.3*	*0.4*	*0.3*	*0.02*	*0.2*
Overall Mean	4.7	12	90	78	49.9	1.1
s.e	0.3	1.3	6.5	7.2	2.7	0.1

8.4 DISCUSSION

8.4.1 Provisioning attendance

During chick rearing parents undertook a cyclical foraging strategy of long trips (5-23 days) followed by shorter trips (daily for 2-5 days). Weimerskirch (1998) also described this strategy for Light-mantled sooty albatrosses on Isle Crozet and noted that it was probably related to the location of different prey items and energetic requirements during different stages of the breeding cycle. He suggested that the birds were feeding in oceanic waters on the long trips and in shelf waters on the shorter trips. It is likely that the same factors are influencing attendance patterns on Macquarie Island, and instead of feeding around a shelf edge (there is no 'shelf' as such around Macquarie Island) during the short trips, these birds are probably feeding around localised "hot spots" of oceanic production over deep sea ridges beneath the surface (e.g. similar to Black-browed albatrosses - see Chapter 7).

Several species of Procellariforme utilise this strategy, and in a review of five species, Weimerskirch *et al.* (1994a) suggested that the short trips allow a parent to provide the chicks with increased amount of food in a short period of time. However, these authors found that short trips are energetically expensive for the parent and it long trips are necessary to allow the parents to regain condition and continue provisioning the chick successfully (Weimerskirch *et al.* 1994c; Weimerskirch *et al.* 1999; Catard *et al.* 2000). Such a partitioning of resources during provisioning may also reduce the dependence of parents on distant food resources and allow more consistent delivery of nutrition to the chicks.

8.4.2 Chick provisioning

Light-mantled sooty albatross chicks were fed on average 518 g of food at each feeding event, which occurred on average every 1.4 – 1.6 days. Due to the foraging strategy described above, chick were often fed successive meals within hours of each other, or at the opposite end of the spectrum, occasionally fasted for up to ten days at a time. Mean meal size was consistent throughout the provisioning period and the rate at which a chick was provisioned decreased after the chick achieved peak weight as the feeding frequency decreased. This decrease in feeding frequency might be attributable to the deteriorating condition of the parent as the provisioning regime progressed and consequently, longer foraging trips may have been required to maintain adequate condition (Weimerskirch 1986). There were no significant

differences in the overall provisioning parameters between years (i.e. locations) and all chicks on automatic weighing nests fledged successfully.

8.4.3 Chick Growth

8.4.3.1 Growth to peak weight

Light-mantled sooty albatross chicks displayed a relatively typical procellariiform growth pattern with a rapid exponential increase in weight observed after the brood-guard until the chick was around 60 days old, followed by a period of slower growth as chick reached their peak mass. Even though Gompertz growth curves fitted data from the whole provisioning regime well, when fitted to the 'growth to Day-85 data' a significantly better fit was observed. This probably reflects the inability of a positive Gompertz curve to accurately model the decline in weight during the mass recession period.

8.4.3.2 Mass recession period

Mass recession in fledgling birds is a well-known phenomenon (e.g. see Ricklefs 1968b) but few studies have quantified data from this period, particularly for Procellariiformes. Huin and Prince (2000) combined a positive and negative Gompertz curve and showed that it could be used to adequately describe growth throughout the whole provisioning period in Black-browed and Grey-headed albatrosses from Bird Island. This curve did not fit the growth data from the Light-mantled sooty albatross chicks (r^2 = 0.1-0.2) and this may be due to the significant fluctuations in mass throughout this period due to the combination of episodic and intense feeding events that characterised this period of the provisioning regime.

8.4.3.3 Contribution of each parent

Although the amount of food delivered by each parent was relatively consistent, some disparity was noted in the provisioning regime of one chick in 1999/00. Croxall and Ricketts (1983) showed that Wandering albatross chicks were less likely to fledge if there was an unequal contribution by each parent. This was not found to be the case with the Light-mantled sooty albatrosses as all chicks fledged at a similar age and weight despite some disparity in provisioning regimes. Huin *et al.* (2000) also found that provisioning rate of the parents did not influence the fledging age of Grey-headed and Black-browed albatross chicks. Studies on Wandering albatrosses showed that male parents delivered more food to chicks and provisioned chicks at different rates (Weimerskirch *et al.* 2000a; Weimerskirch and Lys 2000). These studies also demonstrated that male and female chicks were provisioned differently. These sex based provisioning differences may be a factor in the variation

observed in the provisioning strategy of Light-mantle sooty albatrosses on Macquarie Island; however, this species is not as sexually dimorphic as Wandering albatrosses and therefore such sex based differences are likely to be less obvious.

8.4.4 Comparison of provisioning regime with other species

Provisioning and growth parameters of eight albatross species are summarised in Table 8.7. It appears that the foraging strategy utilised during the provisioning regime is a major factor in the amount and frequency of food delivered to each chick. Grey-headed albatrosses, which tend to forage primarily in pelagic waters for squid (Huin *et al.* 2000; Waugh *et al.* 2000) fed their chick less frequently than Black-browed, Campbell and Shy albatrosses, which tend to forage over more neritic waters during their provisioning regimes (Weimerskirch 1997a; Waugh *et al.* 2000; Huin *et al.* 2000; Hedd *et al.* 2002). Light-mantled sooty albatrosses breeding on Macquarie Island, which undertook relatively long trips (i.e. up to 20 days in length) as part of their cyclic alternating foraging strategy, fed chicks the least frequently of the smaller albatross species, and were most similar in this respect to the larger Wandering albatrosses (Berrow *et al.* 2000; Weimerskirch and Lys 2000). Such a similarity may seem anomalous, but Light-mantled sooty albatrosses have been described as having one of the more pelagic breeding distributions of all the smaller albatross species (Thomas 1982; Weimerskirch and Robertson 1994; Weimerskirch 1998), and in this respect they are very similar to Wandering albatrosses.

Differences in the mean meal size delivered to the chicks of different species also appeared to be related to the foraging strategy and feeding frequency. Biennially breeding species such as Wandering, Grey-headed and Light-mantled sooty albatrosses feed chicks larger meals than annually breeding species (Table 8.7). Light-mantled sooty albatrosses also showed a low chick provisioning rate relative to the other smaller albatross species and this is mainly attributable to the comparatively low feeding frequency. Excluding the large Wandering and Royal albatrosses, Shy albatrosses, the most neritic and frequent feeders, delivered the smallest meals to chicks on average (Hedd *et al.* 2002), whilst Grey-headed albatrosses, that regularly foraged in pelagic waters delivered the largest meals to chicks (Huin *et al.* 2000). Light-mantled sooty albatrosses, which undertake a combination of both long and short foraging trips (similar to Wandering albatrosses -Weimerskirch *et al.* 1997b; Weimerskirch and Lys 2000), delivered a mean meal size that was intermediate between that of the neritic and pelagic feeders.

Table 8.7
Comparison of provisioning and growth parameters for eight species of albatross, listed in descending order of mass at fledging

Location Species (breeding frequency)	Peak Mass (kg) [A]	Fledgling period	Fledging mass (% decrease)	Feeding interval (days)[B]	Mean meal size (g)	Provisioning rate (g day-1) [B]	Growth constant (k)	t_{10} - t_{90} (days)	mean daily mass gain t_{10} - t_{90} (g)	mean daily mass gain t_{10} - t_{90} % asymptotic	Source
Wandering albatross *Diomedea exulans* (biennial)											
South Georgia	12.9 [F]	279 [F]	11.1 (14) [F]	2.5 [F]	960	264 [C]	0.026	164	56.0	0.5	Berrow *et al*. 2000;Tickell 1968; J.P. Croxall unpubl. (cited in Thomas *et al.* 1983)
Iles Crozet	13.4	262	10.0 (25)	2.8	910 - 1330	-	0.025	145	74.5	0 4	Weimerskirch and Lys 2000; Weimerskirch *et al.* 2000a; Weimerskirch *et al*. 1986
Northern royal albatross *Diomedea sanfordi* (biennial)											
New Zealand	10.9	236	8.8 (19)	-	-	-	-	105	83.0	0.8	Richdale, 1952
Shy albatross *Thalassarche cauta* (annual)											
Tasmania	5.5	127	5.0 (9)	0.9	372	399	0.035	80	58.3	1	Hedd *et al.* 2002 [G]
Black-browed albatross *Thalassarche melanophrys* (annual)											
South Georgia	4.7	116	3.5 (25)	-	-	-	0.048	64 [H]	70.0	1.4	Ricketts and Prince, 1981; Tickell and Pinder 1975
South Georgia	4 6[D]	116	-	1.2	569	542	0.042	-	-	-	Huin *et al.* 2000 [G]
Grey-headed alabtross *Thalassarche chrysostoma* (biennial)											
South Georgia	4.7	141	3.4 (28)	-	-	-	0.042	73 [H]	63.0	1.3	Ricketts and Prince 1981; Tickell and Pinder 1975
South Georgia	4.5[D]	141	-	1.3	616	539	0.037	-	-	-	Huin *et al.* 2000 [G]
Yellow-nosed albatross *Thalassarche carteri* (annual)											
Iles Kerguelen	3.5	115	-	-	-	-	-	54	50.0	1.5	Weimerskirch *et al.* 1986; Jouventin 1983
Light-mantled sooty albatross *Phoebatria palpebrata* (biennial)											
Macquarie Island	4.6	141	3.1 (33)	1.5	517	343	0.037	78	50.0	1.1	This study [G]
South Georgia	3.4	141	2.6 (25)	2.2 [E]	700	-	-	62	45.0	1.3	Thomas *et al.* 1983
Iles Crozet	-	157	-	2.9	-	-	-	67	42.0	~1.3	Weimerskirch *et al.* 1986
Sooty albatross *Pheobatria fusca* (biennial)											
Iles Crozet	3	164	-	-	-	-	-	69	37	1.32	Weimerskirch *et al.* 1986

[A] Actual mean peak mass except where indicated
[B] From end of brooding to peak mass
[C] From end of brooding to fledging
[D] Peak mass estimated by fitting Gompertz equations
[E] From chick age 20 to 100 days
[F] Calculated from data in Berrow *et al*. 2000
[G] Studies that obtained data using automatic weighing nests
[H] Calculated from Gompertz parameters in Ricketts and Prince 1981

In addition to differences in the overall provisioning parameters of the eight albatross species, there are also differences in temporal trends. The mean meal mass delivered to Black-browed and Shy albatross chicks increased up to the age of around 80-100 days until the chick fledged (Huin *et al.* 2000; Hedd *et al.* 2002) while the mean meal size delivered to Grey-headed albatross chicks increased more rapidly, peaking at around 50-59 days of age and then remaining stable until the chicks were around 100 days old before declining (Huin *et al.* 2000). In contrast to both these trends, the mean meal size delivered to Light-mantled sooty albatross chicks on Macquarie Island remained stable for the entire provisioning period. Most species showed an increase in the time between feeds as the chicks grew older but Shy albatrosses maintained the most consistent provisioning rate for the entire provisioning period (Hedd *et al.* 2002). Black-browed and Grey-headed albatrosses showed a decrease in the provisioning rate that followed a similar pattern to the pattern of variation in mean meal size (Huin *et al.* 2000). The provisioning rate of Light-mantled sooty albatross chicks showed the most marked decline of the four species reflecting the consistency in meal size that occurred concurrently with the increase in time between feeds.

In light of the above parameters and trends, it appears that Grey-headed albatrosses and Light-mantled sooty albatrosses are similar, while Black-browed and Shy albatrosses also share many common aspects of provisioning. While there are also several similarities between the overall provisioning regimes of Light-mantled sooty albatrosses and Wandering albatrosses, Grey-headed albatross chicks fledge at a similar age to Light-mantled sooty albatross chicks (Table 8.7) and comparisons between the two species are probably the most meaningful. Huin and Prince (2000) showed that Grey-headed albatrosses reached a mean peak mass of 4.5 kg after 80 to 100 days, which was very similar to Light-mantled sooty albatrosses (4.6 kg) on Macquarie Island. Both Grey-headed and Light-mantled sooty albatrosses show similar patterns of breeding frequency and it seems likely that aspects of life history such as provisioning regimes and breeding frequency are strongly interrelated.

Provisioning strategies are variable both between and within species, and appear largely driven by: a) the distance that a species travels to forage, b) the body size of the species and c) a complex combination of interrelated life-history attributes such as breeding frequency and 'individual quality' of individuals. Therefore it may be possible to characterise the provisioning regime of a species if enough of the above factors are known. However, in addition to these factors, provisioning regimes are also influenced by the need for a parent to maintain its own condition while fulfilling the energetic requirements of a chick and consequently, provisioning rates often vary significantly within a species (Huin *et al.* 2000; Berrow 2000; Weimerskirch *et al.* 2000a; Hedd *et al.* 2002).

Studies on Wandering albatrosses have shown that the age and breeding experience of a pair also influences the provisioning regime (Lequette and Weimerskirch 1990; Berrow *et al.* 2000). Although no differences were found in the mean meal size or feeding frequency in these studies, experienced birds undertook shorter 'long' foraging trips and spent more time attending the nest (Berrow *et al.* 2000). These studies supported the hypothesis that individual parents are competent foragers when they start breeding; however, it takes some months for inexperienced birds to adapt to the additional burden of the nutritional requirements of the chick. Some of the inter-nest variation observed between individual nests in the current study may be attributable to the different levels of experience of the parents. Other studies have also shown that male and female wandering albatrosses provision the chick at different rates (Weimerskirch 1995; Weimerskirch *et al.* 2000a), and while Light-mantled sooty albatrosses are not as sexually dimorphic as this larger species, it is still possible that the sex of a parent may influence the provisioning parameters.

Weimerskirch *et al.* (2000c) examined the manipulated foraging responses of artificially handicapped adults and nutritionally underfed chicks in Yellow nosed albatrosses. This study demonstrated that the parent is aware of the nutritional needs of the chick, however, it could only increase feeding if it has sufficient reserves of its own. In a similar study on Black-browed albatrosses, Weimerskirch *et al.* (1997c) also suggested that there is significant variation in the ability of different species to adjust provisioning regimes but demonstrated that species that forage in more pelagic areas are likely to have greater regulatory ability. However, Hedd *et al.* (2002) interpreted their results as evidence that Shy albatrosses (a frequent and neritic forager) do respond to the demands of hungry chicks.

The alternative long and short trips that typify the provisioning strategy exhibited by Light-mantled sooty albatrosses result in a relatively low frequency of feeds, although the mean size remained relatively consistent as the chick grew older. Weimerskirch *et al.* (1993) suggested that a combination of long and short foraging trips by Wandering albatrosses might be based on the need to simultaneously satisfy the two conflicting demands. Weimerskirch *et al.* (1994a) expanded this argument to include four pelagic Procellariiformes. It is likely that the Light-mantled sooty albatrosses are utilising the same strategy for similar reasons. It is possible that the longer trips allow the parents to build up its own condition allowing it to return to the island and make frequent (up to three times in one day) provisioning visits to satisfy the requirements of the chick.

It is possible that Light-mantled sooty albatrosses are also good regulators of food supply to chicks and that the number and frequency of daily trips observed after long foraging trips are in response to the nutritional needs of the chick. The apparent increase in feeding frequency of one parent and the concurrent low frequency rate of the other also provided evidence that Light-mantled sooty albatrosses are capable of responding to the nutritional state of a chick by increasing feeding frequency. The provisioning data suggests that the amount of food brought back each time is limited by physiological factors and it is possible that the only way that parents can feed the chick more food over time is to increase the feeding frequency, particularly of the short trips.

8.4.5 Comparisons of chick growth with other species

Generally, larger size has been associated with a slower growth rate (Pennycuick *et al.* 1984) and this appears holds true for the albatrosses compared in Table 8.7. For example, the medium sized Shy albatross grows more quickly than the Wandering albatross, and more slowly than the smaller species of albatross (Table 8.7). The variation in growth rate between the similarly sized Light-mantled, Black-browed and Grey-headed albatrosses is likely to be related to the provisioning rate (Table 8.7), which typically reflects foraging strategy of each species. The maximum growth rate (k in Table 8.7) of Light-mantled sooty albatross chicks was exactly the same as for the Grey-headed albatrosses and both species achieved this maximum rate at a mean of 30 days of age (Huin *et al.* 2000). The absolute growth rate of Light-mantled sooty albatross chicks reported here is slightly higher, and a longer time was taken to reach 90% of asymptotic body mass than that reported by Weimerskirch *et al.* (1986) (Table 8.7); however, the methodology used to calculate these rates were quite different in the two studies which may complicate direct comparisons.

The growth rate between 10% and 90% of asymptotic mass also provides a basis for comparison between species as it reflects the growth of the chick in the context of its eventual size. Light-mantled sooty albatross chicks took the longest of all the smaller albatross species to grow through this time period, and again showed the most similarities with the Grey-headed albatross (Table 8.7). Larger species, such as the Wandering albatross, that take a significantly longer time to fledge a chick, took much longer to grow to 90% of asymptotic mass and the corresponding percentage mass increase was also low. Estimates of the mass recession rates of Black-browed and Grey-headed albatrosses (43.3 ± 5.0 $g.day^{-1}$ and 21.4 ± 2.8 $g.day^{-1}$ respectively - Huin and Prince 2000) were not significantly different from that observed in the Light-mantled sooty albatross chicks (26.9 ± 5.8 $g.day^{-1}$), particularly in the case of Grey-headed albatrosses.

Overall provisioning rates of Light-mantled sooty albatross chicks were not correlated with growth rate, and a similar lack of consistent correlation has been found in other studies (Huin and Prince 2000; Weimerskirch and Lys 2000; Hedd *et al.* 2002). A provisioning-growth association was identified in Grey-headed albatrosses by Huin *et al.* (2000), but appeared to be largely driven by atypically low growth in 1994, which was notable for poor food availability (Croxall *et al.* 1999b). Clearly provisioning regimes and growth rates are influenced by the complex interaction of several life history attributes. Fundamental life-history attributes such as body size and breeding frequency appear to initially define the growth rates, and to a slightly lesser extent the provisioning regime of a species. Life histories are also closely tied in with the distribution of a species. Species that breed in temperate regions, such as Shy albatrosses, have been included in comparisons with more southerly subantarctic species here, but the different areas in which they breed and the influence that this has on the evolution of life-histories may also confound meaningful comparisons.

Foraging ecology, available food resources and the foraging efficiency (related to the 'quality' of the individual) are also likely to be critical in determining how often a chick gets fed and how quickly it will grow. However, aspects such as foraging ecology are inextricably linked to fundamental life-history attributes (Boggs 1992, Chapters 5 and 7) further complicating the assessment of consistent mechanisms underlying provisioning regimes or patterns of growth. The complexity of these interactions is highlighted by the comparisons between species presented in Table 8.7 and it may be impossible to reconcile particular provisioning regimes or growth rates with specific physiological or biological factors of albatrosses in general. The provisioning and growth regime has been adequately explained in this context for some species (Prince and Ricketts 1981; Weimerskirch *et al.* 1986; Huin *et al.* 2000; Weimerskirch and Lys 2000; Hedd *et al.* 2002) and from the results presented here, Light-mantled sooty albatrosses from Macquarie Island can also be included amongst these species.

APPENDIX 8.1

Growth curves fitted to Light-mantled sooty albatross chick data

1, 2, 3 from following Richards (1959), Brown and Rothery (1984) and 4. from Huin (2000)

1. Logistic $$W(t) = \frac{A}{[1 + e^{-k(t-t1)}]}$$

2. von Bertalannfy $$W(t) = A\,[\,1 - e^{-k(t-t1)}\,]^{3}$$

3. Gompertz $$W(t) = A\, e^{-e^{-k(t-t1)}}$$

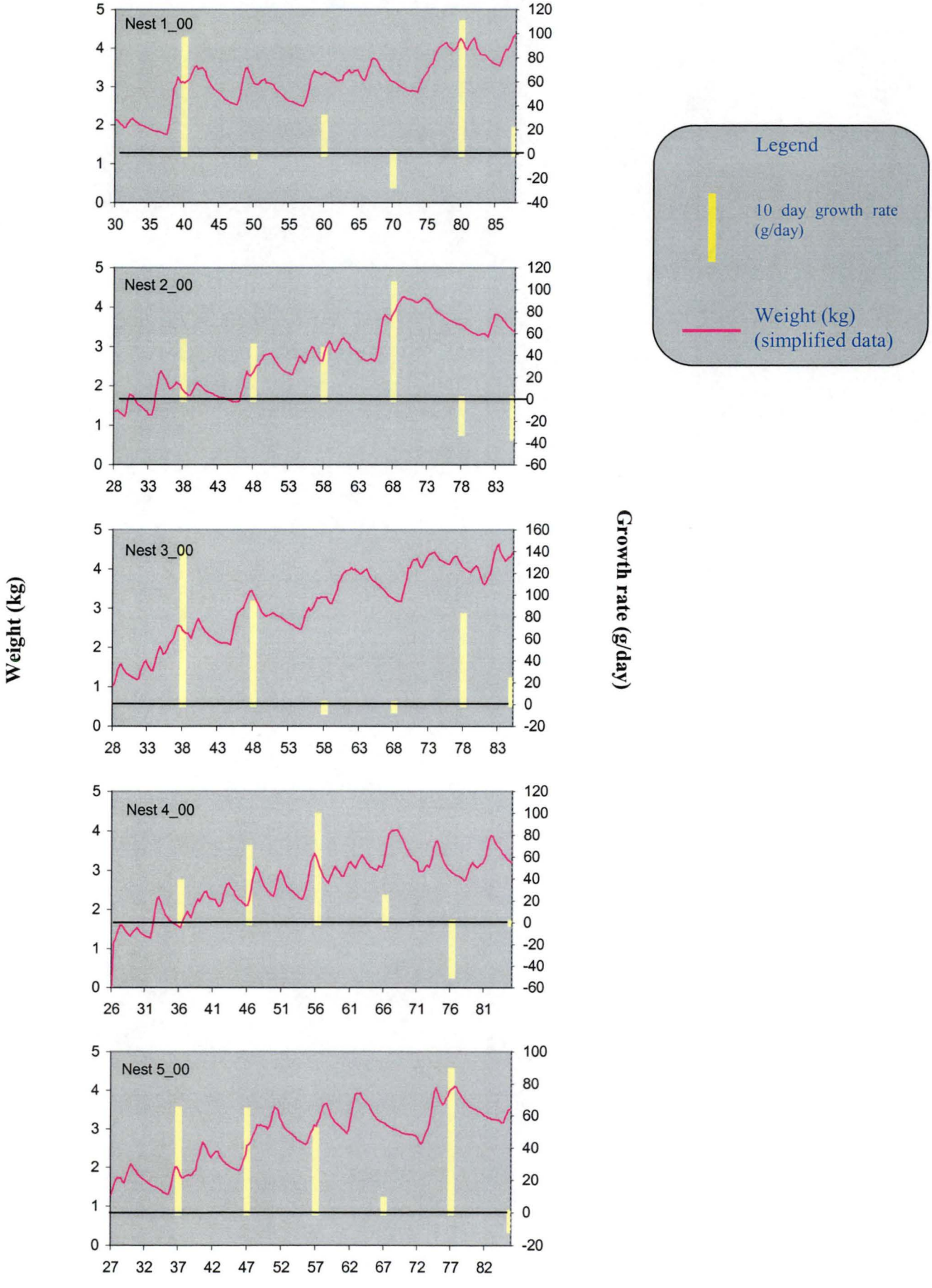
4. Double Gompertz $$W(t) = A\, e^{(-e^{-k1(t-t1)} - e^{k2(t-t2)})}$$

Key

W(t)	weight at time t
A	asymptotic mass
k	constant growth rate factor
k1	constant positive growth rate factor
k2	constant negative growth rate factor
t1	time of fastest growth rate
t2	time of fastest negative growth rate

Appendix 8.2

Weight increases (simplified data) and concurrent growth rates of Light-mantled sooty albatross chicks up to 85 days of age in 2000/01



Chapter 9 – General Discussion

9.1 RATIONALE OF THE ALBATROSS STUDY ON MACQUARIE ISLAND

There was considerable incentive to initiate a study into albatrosses on Macquarie Island in the early 1990's. Firstly, throughout the 1980's and early 1990's concerns began to mount about the potential impact of elevated mortality of albatrosses and the number of birds that were being caught and killed in long-line fisheries. Brothers (1991) was one of the first to quantify the extent of this impact and several other studies around this time showed that population declines in many albatross populations around the globe could be attributable to extra mortality caused by interactions with long-line fisheries (Weimerskirch and Jouventin 1987; Croxall *et al.* 1990; Prince *et al.* 1994). The prevalence of these declines were comprehensively documented by Gales (1993) and consequently the study of albatross populations about which little was known became a priority.

A brief study in the 1980's identified the fact that the Wandering albatross breeding population on Macquarie Island was declining (Tomkins 1985b), and population modelling was used to estimate the extent of this decline and show that it was likely to be attributable to extra mortality from interactions with long-line fisheries (de la Mare and Kerry 1994). A six-year study in the late 1970's and early 1980's reported on breeding numbers of Black-browed and Grey-headed albatrosses on Macquarie Island and also discussed the breeding success of these species (Copson 1988). Although Light-mantled sooty albatrosses had been banded and studied for two decades on Macquarie Island few published data exist apart from a brief synopsis of some aspects of breeding biology (Kerry and Garland 1984). The status of the breeding populations on Macquarie Island was largely unknown when long-line fishing was identified as a major threat to albatrosses worldwide, and in light of the paucity of data on these species and the potential risk to the small populations, a comprehensive program into the population demographics, breeding biology and foraging ecology was initiated on Macquarie Island.

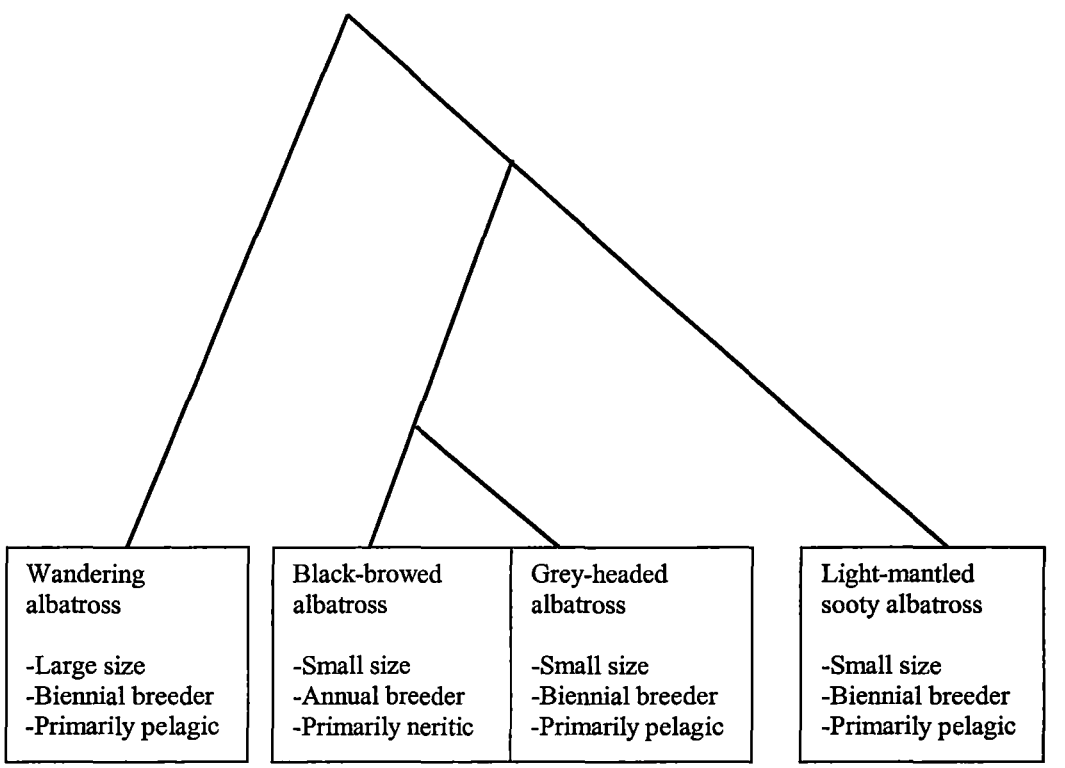
A secondary aim of the project, which is a subset of, and inextricably linked to the first, was to address the paucity of information on these species breeding on Macquarie Island in the context of the global pool of information on albatross populations worldwide, particularly in the subantarctic region. While obtaining data on past, present and future population trends and forging ecology is of most use in assessing the impact and risk of long-line fisheries, data on other life history aspects are also necessary to determine the conservation status of a species

and assess if there are differences between populations breeding at different locations (Croxall 1998).

9.2 THE SPECIES

Using biogeographic distributions and morphometric measurements the extant albatross taxa can be classified into one of four broadly defined groups: 1) the North Pacific Albatrosses, 2) the Great Albatrosses, 3) the Southern Mollymawks and 4) the Sooty Albatrosses (Warham 1990; Robertson and Nunn 1998). The Great Albatrosses (including Wandering albatrosses *Diomedea exulans*) diverged early from the Southern Mollyawks (including the Black-browed albatrosses *Thalassarche melanophrys* and Grey-headed albatrosses *Thalassarche chrysostoma*) and Sooty Albatrosses (including Light-mantled sooty albatrosses (*Phoebetria palpebrata*) (Robertson and Nunn 1998). In evolutionary terms, the latter two groups diverged later again from a common ancestor (Robertson and Nunn 1998, Figure 9.1).

Figure 9.1
Simplified phylogenetic relationships and characteristics of the four species of albatross breeding on Macquarie Island (following Robertson and Nunn 1998)



Representatives of three of the four main groups are found on Macquarie Island, and the results from the current study are consistent with these phylogenetic distinctions. The marked differences between the Wandering albatrosses (for example body size and breeding cycle) and the smaller albatrosses are consistent with an early phylogenetic diversion. Similarly, the shared characteristics of the three smaller albatross species may be attributable to their having a common ancestor. However, the Southern Mollymawks are recognised as the most morphologically diverse taxon and have evolved foraging regimes that allowed annual breeding cycles to develop (Robertson and Nunn 1998). As a result, Black-browed and Grey-headed albatrosses, which are almost identical in size, have quite different breeding cycles and in addition appear to respond quite differently to fluctuations in oceanic resources (Prince *et al.* 1994; Weimerskirch *et al.* 1997c; Waugh *et al.* 1999a; Nel *et al.* 2001, Chapters 4, 5, 6, 7).

Light-mantled sooty albatrosses have evolved a wide ranging pelagic distribution during the breeding season (Thomas 1982; Weimerskirch and Robertson 1994; Weimerskirch 1998, Chapters 6, 8); however, it also utilise near-shore waters on a regular basis during the chick-provisioning regime. The similar life history attributes of the Light-mantled sooty and Grey-headed albatrosses (e.g. Chapters 5, 6, 8) are an example of convergent evolution of a primarily pelagic foraging strategy. However, the extremely long distances travelled by Light-mantled sooty albatrosses, coupled with the cyclical nature of their provisioning regime are unique to this species and are indicative of the relatively early phylogenetic diversion from the Black-browed and Grey-headed albatrosses (Figure 9.1).

The above discussion highlights two main issues. Firstly, each albatross species breeding on Macquarie Island is distinct from the others, both in terms of life history attributes and foraging ecology. Secondly, the foraging strategies exhibited by a species are one of the most influential factors on aspects of life-history and changes in demographic parameters, controlling much of the evolutionary variation in life-history, and likely to still impact upon annual variation in those factors today (Chapters 4, 5, 6, 7, 8). Consequently, it is critical that conservation management addresses each species on an individual basis and that management strategies are based on changes in life history attributes and demographic data (from long-term studies on population dynamic and breeding biology), coupled with information on foraging ecology. Recent work on the genetic structure of individual albatross populations has shown that the terminal taxa identified by Robertson and Nunn (1998) may be further partitioned (e.g. Burg 2000, Mike Double, unpublished data). In this context it may be more appropriate to formulate conservation strategies in response to the status of individual populations rather than in response to the global status of a species.

9.2 THE GLOBAL POOL OF DATA

9.2.1 Overview

Long-term comprehensive studies on subantarctic populations of albatrosses have been conducted on French islands in the southern Indian Ocean and by British researchers on South Georgia in the Atlantic Ocean since the 1970's. The information and publications that have been produced by these studies has not only illustrated the impact of long-line fisheries on albatross populations (e.g. see Croxall *et al.* 1998; Weimerskirch *et al.* 1998) but also contributed greatly to our knowledge of the breeding biology and foraging ecology of albatrosses in general (e.g. see Croxall 1979; Prince 1980; Weimerskirch *et al.* 1986; Weimerskirch *et al.* 1987; Jouventin and Weimerskirch 1988; Croxall *et al.* 1990; Croxall 1991; Weimerskirch *et al.* 1992; Prince *et al.* 1994; Weimerskirch *et al.* 1994a; Prince *et al.* 1999).

More recently, subantarctic studies have documented population dynamics, breeding biology and foraging ecology of albatrosses on New Zealand subantarctic islands (e.g. Walker and Elliott 1999; Waugh *et al.* 1999a; Waugh *et al.* 1999b; Stahl and Sagar 2000a; Waugh *et al.* 2000) and South African Marion Island in the Indian Ocean (Nel *et al.* 2000; Nel *et al.* 2001; Nel *et al.* 2002a). Studies on critically endangered species such as the Amsterdam albatross (*Diomedea amsterdamensis*) have also highlighted the importance of monitoring studies in identifying populations that are at risk (Weimerskirch *et al.* 1997a; Inchausti and Weimerskirch 2001). The above list by no means encapsulates all research done on the conservation of albatrosses globally (see Table 9.1 for more comprehensive summary, including species with a more temperate distribution); however, it does indicate the breadth of knowledge that has been, and is being accumulated, particularly in the subantarctic. Nevertheless, there are still significant gaps in our knowledge, particularly at the population level, upon which confident assessment of global status depends.

9.2.2 Gaps in the global pool of data

Comparisons here are largely restricted to subantarctic populations, being the most comparable to the Macquarie Island populations under investigation in the current study. Well established, long-term studies such as those on South Georgia, Iles Crozet, Campbell Island and Marion Island have generated a wealth of information that has been used to assess the status of the individual populations at these locations (e.g. see reviews in Croxall *et al.* 1998; Prince *et al.* 1998; Weimerskirch 1998; Weimerskirch *et al.* 1998, Waugh *et al.* 1999b; Nel *et al.* 2002a). However, even these studies are not exhaustive.

Table 9.1

Summary of the global pool of data on some of the more studied albatross population worldwide

Comparable data is used wherever possible and most sample sizes, standard deviations and/or standard errors can be found in the summary tables in the relevant chapters

	The study		Population demographics						Breeding biology				Breeding Frequency						Chick provisioning				Foraging areas (pelagic - oceanic; neritic - shelf or coast based)				
Species \ Location	Duration of study (intensive in brackets)	Approx. colony size	time period	adult survival %	fledgling survival %	hatching success %	chick success %	mean overall success %	inc. period (days)	mean inc. shift (days)	brood-guard period (days)	mean brood guard shift (days)	typical breeding frequency	succ. n+1	succ n+2	succ. n+3	unsucn +1	unsucn +2	unsuc n+3	feed interval (days)	mean feed (g)	growth constant (k)	chick fledge (days)	inc.	brood guard	chick rearing	non-breeding season	Source
Wandering albatross (*Diomedea exulans*)																											
Ile Crozet	35	1700	1966 - 1995	93.1	38 2	84	91	69	78	12 6	33	2 8	Biennial	0	89	6	84	10	3	2 8	-	0 025	271	pelagic	neritic	both	mostly pelagic	1,2,3,6,7,8,9,10,11,12,14,20,21, 37
South Georgia	30	2100	1976 - 1993	91 9	48 9 - 52.4	73	87	64	78	21	32	2 6	Biennial	0	66	13	63	17	8	2.5	960	0.026	272-284	pelagic	neritic	both	-	1,4,5,13,15,16,17,18, 19
Marion Island	20	1800	-	-	-	-	-	-	-	7.5	-	2.7	Biennial	-	-	-	-	-	-	-	-	-	-	pelagic	neritic	both	-	1, 22
Macquarie Island	50 (7)	19	1956 - 2000	95 3	45.9	64	93	60	79	8 8	30	3.1	Biennial	0	89	4	90	4	0	-	-	-	-	-	-	-	-	this study
Wandering albatross (*Diomedea gibsonli*)																											
Adams Island	10	5800	1993 - 1995	97	-	-	-	67	-	-	-	-	Biennial	-	-	-	-	-	-	-	-	-	-	pelagic	both	-	-	1, 23, 24
Amsterdam albatross (*Diomedea amsterdamensis*)																											
Amsterdam Island	13	13	1982- 1995	96	70	-	-	72	76-83	7.5	27	2 5	Biennial	-	-	-	-	-	-	-	-	-	261	-	-	-	-	1, 37, 38
Black-browed albatross (*Thalassarche melanophris*)																											
Iles kerguelen	24	3100	1979 - 1995	91	14	-	-	63	-	-	22	-	Annual	-	-	-	-	-	-	1.0	449-543		125	-	-	neritic	-	1,2,11,8, 12
Bird Island	26	96 000	1976 - 1993	92	15	62	43	24	68	13.2	22	2 5	Annual	81	7	3	75	9	3	1.3	569	0 042	116	neritic	neritic	neritic	neritic	1,4,26,27,28,18
Macquarie Island	30 (7)	42	1976 - 2000	92	59	54	85	46	69	3.3	22	1.7	Annual	85	6	0	78	1	2	-	-	-	110-127	-	-	-	-	this study
Black-browed albatross (*T. impavida*)																											
Campbell Island	20 (12)	26 000	1984 - 1996	95	29	86	79	66	-	-	-	-	Annual	83	7	1	74	8	1	0 8	393 - 474	-	-	both	neritic	mostly neritic	-	1,29,30,31
Grey-headed albatross (*Thalassarche chrysostoma*)																											
Iles Kerguelen	22 (-)	7900	-	-	-	-	-	-	73	9.2	23	2 4	Biennial	-	-	-	-	-	-	-	-	-	145	-	-	-	-	1,8
South Georgia	25	54 000	1977 - 1993	93	19	60	65	39	72	11 8	23	2.9	Biennial	1	68	11	54	23	5	1.2	616	0.037	141	-	-	mostly pelagic	pelagic	1,4,18,25
Marion Island	20 (?)	6200	-	-	-	-	-	-	-	19.3*	-	3.5-3 7	Biennial	-	-	-	-	-	-	-	-	-	-	pelagic	mostly neritic	-	-	1,32,33
Campbell Island	15 (12)	6400	1984 - 1996	95	24	80	51	40	-	-	-	-	Biennial	2	62	8	72	13	3	1.1	456 - 542	-	-	pelagic	mostly neritic	mostly pelagic	-	1,29,30,31
Macquarie Island	30 (7)	110	1976 - 2000	97	31	69	80	55	72	5 8	25	2.5	Biennial	4	56	13	61	17	2	-	-	-	128-143	pelagic	mostly neritic	-	-	this study
Sooty albatross (*Pheobetria fusca*)																											
Iles Crozet	34 (9)	2300	1966- 1995	90	22	-	-	58	71	11	21	2.3	Biennial	0	83	13	83	13	3	-	-	-	164	pelagic	pelagic	pelagic	-	1,8,11,12,34
Marion Island	2	2000	-	-	-	-	-	17	70	8	21	1 9	Biennial	-	-	-	-	-	-	2.4	-	-	149-164	-	-	-	-	1, 35
Light-mantled sooty albatross (*Pheobatria palpebrata*)																											
Iles Crozet	36 (10)	2100	1966 - 1995	97	-	-	-	35	68	11.3	-	-	Biennial	0	75	12	59	25	12	2.9	-	42	150	pelagic	mostly pelagic	-	-	1,8,11,12,34
South Georgia	2	6500	-	-	-	-	-	47	70	12 3	20	2.7	Biennial	-	-	-	-	-	-	2 2	-	-	-	-	-	-	-	1, 36
Marion Island	2	200	-	-	-	-	-	31	67	12.5	20	2 8	Biennial	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1, 35
Macquarie Island	20 (7)	1500	-	-	-	-	-	51	67	10.5	20	2.1	Biennial	1	61	6	57	16	7	1.5	517	0 037	141	pelagic	-	-	-	this study, 52
Shy albatross (*Thalassarche cauta*)																											

Table 9.1

Summary of the global pool of data on some of the more studied albatross popualtion worldwide

Comparable data is used wherever possible and most sample sizes, standard deviations and/or standard errors can be found in the summary tables in the relevant chapters

	The study		Population demographics						Breeding biology				Breeding Frequency						Chick provisioning				Foraging areas (pelagic - oceanic; neritic shelf or coast based)				
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Albatross Island	25	5000	-	-	-	-	-	35	73	2 9	15-30	2 4	Annual	-	-	-	-	-	-	0.9	371	0.035	127	neritic	neritic	neritic	neritic	1, 39, 40
Indian Yellow nosed albatross (*Thalassarche carteri*)																												
Amsterdam Island	24 (7)	25 000	1978 - 1995	86	15	-	-	24.5	-	12-15	-	-	Annual	93	5	2	88	10	2	-	400-500	-	115	-	-	pelagic		1, 8, 11, 12, 41, 42
Bullers albatross (*Thalassarche bulleri*)																												
Snares	10 (2)	8500	-	-	-	78	74	57	69	10	18-30	-	Annual	90	-	-	-	-	-	-	-	-	167	mostly pelagic	mostlt neritic	both		1, 43, 44
Laysan albatross (*Pheobastria immutabills*)																												
Midway Atoll	40 - sporadic	427 000	-	-	-	-	-	-	66	7 7	19	2.1	Annual	76			90+			-	-	-	-	-	-	-	-	49, 51
Black-footed albatross (*Diomedea nigripes*)																												
Midway Atoll	40 - sporadic	20 500	-	-	-	-	-	-	64	13	17	1.9	Annual							-	-	-	-	-	-	-	-	48, 49, 50
Waved albatross (*Diomedea irrorata*)																												
Galapogas Islands	sporadic	15 500	-	-	-	10-56	-	-	61	20	-	2 3	Annual	-	-	-	-	-	-	-	-	-	-	mostly neritic	-	-	-	45, 46, 47

1 - SC-CCAMLR-XX 2001 - Table 49

2 - Weimerskirch and Jouventin 1998

3 - Weimerskirch 1992

4 - Croxall et al. 1998

5 - Croxall et al. 1990

6 - Weimerskirch and Jouventine 1987

7 - Weimerskirch 1992

8 - Weimerskirch et al 1986

9 - Weimerskirch et al 1993

10 - Weimerskirch 1995

11 - Jouventin and Weimerskirch 1988

12 - Weimerskirch 1998

13 - Croxall et al. 1992

14 - Weimerskirch and Wilson 2000

15 - Tickell, 1968

16 - Croxall and Rejckets 1983

17 - Croxall, 1991

18 - Prince et al 1998

19 - Berrow et al 2000

20 - Weimerskirch and Lys 2000

21 - Weimerskirch et al. 2000a

22 - Nel et al 2002

23 - Walker and Elliot 1999

24 - Walker et al. 1995

25 - Prince et al 1994

26 - Tickell and Pinder 1975

27 - Prince et al 1981

28 - Croxall et al 1988

29 - Waugh et al. 1999a

30 - Waugh et al. 1999b

31 - Waugh et al. 2000

32 - Nel et al 2000

33 - Nel et al 2001

34 - Weimerskirch et al. 1987

35 - Berruti 1979

36 - Thomas et al 1983

37 - Weimerskirch et al 1997c

38 - Jouventin et al 1989

39 - Hedd et al 2001

40 - Hedd et al 2002

41 - Weimerskirch et al 2000b

42 - Weimerskirch et al 2001

43 - Sagar and Warham, 1990

44 - Stahl and Sagar, 2000

45 - Harris, 1973

46 - Andersen et al 1998

47 - Andersen and Cruz 1998

48 - Birdlife International 2000

49 - Rice and Kenyon 1962

50 - Gould et al 1998

51 - Gales 1998

52 - Weimerskirch and Robertson, 1994

For example, few published data exist on the population dynamics (historical and present) of Grey-headed albatrosses on Iles Crozet and Kerguelen, together thought to comprise around 15% of the global breeding population (Gales 1998). There is also a paucity of information on Grey-headed albatrosses breeding at other locations including Diego Ramirez, and Prince Edward Islands (SC-CCAMLR-XX 2001, Table 49). Similarly, few published data exist on the large populations of Black-browed albatrosses breeding on the Falkland Islands and Diego Ramirez; however, recent studies have clarified many aspects of the foraging ecology (Huin 2002) and population trends (BirdLife International 2001b) of the Black-browed albatrosses breeding on the Falkland Islands.

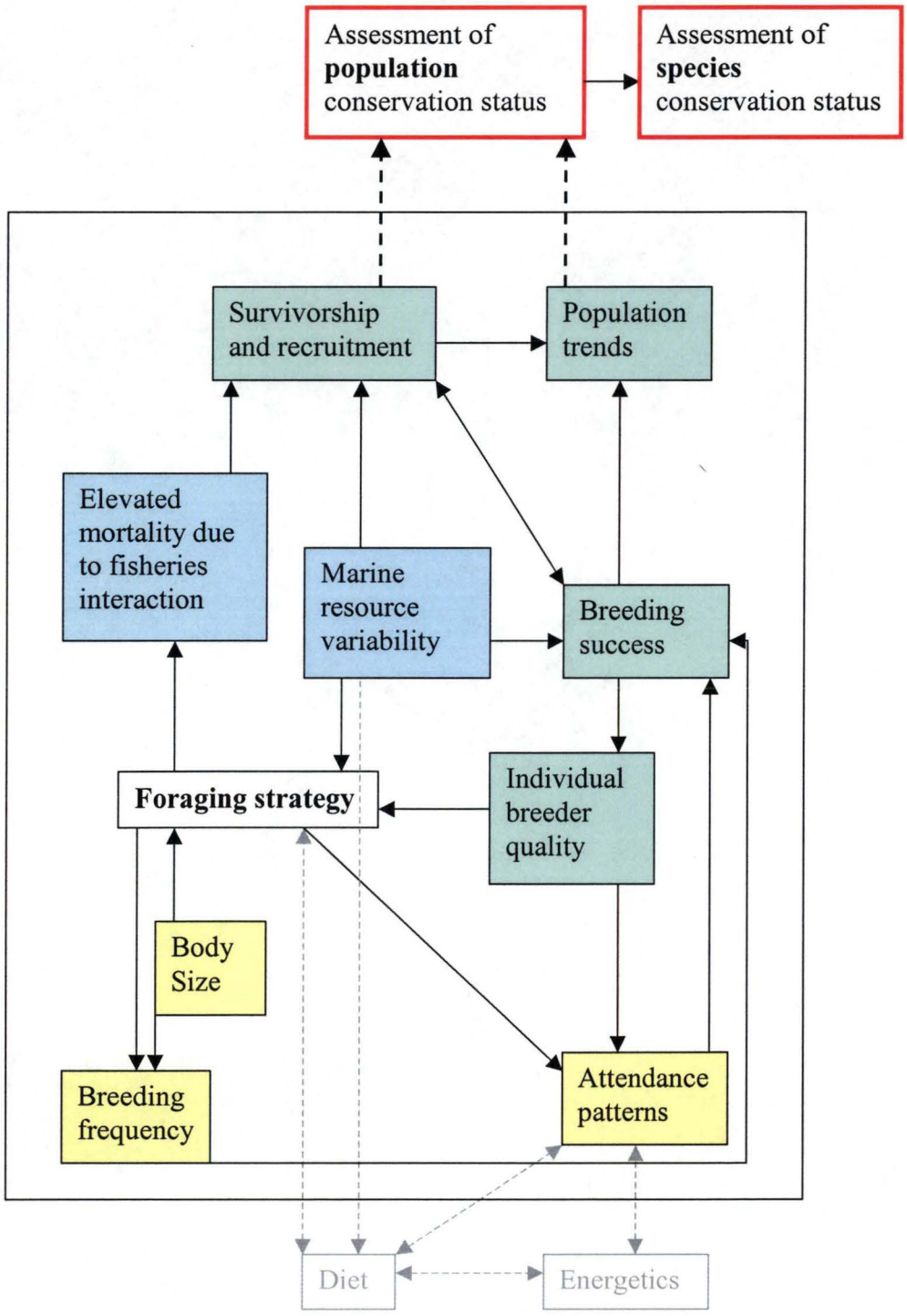
Prior to the advent of the current study very little was know about the population trends of albatrosses breeding on Macquarie Island. Even though these populations are relatively small in comparison to the global populations, the importance of their survival is not diminished, especially in the context of the ongoing genetic work suggesting there may still be more distinct taxa than those described by Robertson and Nunn (1998) (Burg 2000, Moore *et al.* 2001; M. Double unpublished data). Samples for genetic analyses have been collected from the Macquarie Island populations as part of the current study and analyses of these samples is will be useful in establishing the nature of the Macquarie Island populations in the global context. The current study has elevated the level of knowledge about the Macquarie Island albatrosses to one comparable with other well studied subantarctic populations (Table 9.1). In this context this has contributed to the assessment of the global conservation status of these species. Complementing and adding to the existing global data set in this way is critical in assisting global conservation bodies (such as IUCN, BirdLife International and CCAMLR) to focus conservation efforts on the most relevant issues.

9.3 THE CURRENT STUDY

This study has shown that the complex interactions between population demographics, breeding biology, foraging ecology and fundamental life-history attributes are all central to the ability of a species to survive. Foraging ecology in particular plays an important role and the interactions between these parameters are illustrated in Figure 9.1. While presenting a somewhat simplistic view of the complexity, it does assist in following the path to the effective assessment of the conservation status at both the population and species level. Quantifying and describing these life-history attributes, demographic parameters and external influences is the first step in assessing the conservation status of a population. The following discussion summarises the findings of the current study in the context of the links shown in Figure 9.2and compares these aspects with those found in other subantarctic populations.

Figure 9.2
Links between foraging ecology (clear), life-history attributes (yellow), demographic parameters (green) and external influences (blue) leading to the assessment of conservation status (links were established using data from the current study)

Aspects that have not been quantified in the Macquarie Island study are shown in grey



9.3.1 Population demographics and trends

Population trends and estimates of survivorship are amongst the most fundamental parameters required for the assessment of the conservation status of a species (Croxall 1998; Cooper 2000). Currently the breeding population of Wandering albatrosses on Macquarie is stable after a gradual recovery from near extinction levels in the mid-1980's. Survivorship analyses indicated that these declines were attributable to elevated mortality levels of juveniles and adults during the late 1960's and throughout the 1970's. Concurrent trends in the effort of long-line fisheries targeting tuna in the Southern Indian Ocean suggest that these elevated mortality levels were attributable to accidental bycatch on these vessels. Breeding populations in the southern Indian Ocean (e.g. Iles Crozet, Marion Island and Amsterdam Island) showed very similar population trends to the Macquarie Island populations and studies have also linked these declines due to accidental bycatch on long-liners fishing for tuna in the southern Indian Ocean (Weimerskirch *et al.* 1997a; Tuck, G. N. *et al.* 2001; Nel *et al.* 2002a). The current population stability on Macquarie Island is precariously maintained, and any increase in mortality levels could again send this population into steep and irrevocable decline.

The Black-browed albatross breeding population on Macquarie Island appears to have remained stable or increased marginally since the late 1970's. However a smaller colony in the north of the island declined from 31 pairs in the 1950's to one-two pairs in the late 1970's. This provides some evidence that the Macquarie Island Black-browed albatross population underwent a decline, possibly facilitated by elevated mortality levels prior to 1980. This is consistent with the trend in breeding numbers of Campbell albatrosses on Campbell Island. There was no evidence that adult or fledgling survivorship varied temporally since 1976, in contrast to Bird Island, South Georgia, where population declines were attributed to a decrease in juvenile survivorship. The breeding population has remained stable since 1994 at around 40 breeding pairs each year; however, long-line fishing continues to occur and grow in some of the foraging areas of this species (Chapter 7) and due to its small size this population remains at significant risk of decline. Given the recent declines documented in the large Falkland Island populations (BirdLife International 2001b) and the unknown status of large populations breeding off South America (SC-CCAMLR-XX -Table 49), the current conservation status of this species may need to be reviewed and continued monitoring of individual populations is essential in clarifying this status

There is reasonable evidence to suggest that the Grey-headed albatross population has undergone a gradual increase in the order of 1.5-2% per annum since the late 1970's. There was no evidence of time dependent adult or fledgling survivorship since 1976. In contrast to Macquarie Island, Numbers of Grey-headed albatrosses have declined steadily on Campbell Island and Marion Island through the 1970's and 1980's; however, the Marion Island population has subsequently increased since the late 1980's. Breeding numbers on Macquarie Island have remained relatively stable since 1994 although there are relatively high levels of inter-annual fluctuations in the number of eggs laid. Although these trends suggest that this species has not been severely affected by long-line fisheries, like the Black-browed albatross, these populations are at risk from increasing levels from vessels fishing for Patagonian Toothfish in their foraging areas. Like the Black-browed albatrosses there are still large breeding populations for which very little is known (e.g. the Prince Edward Islands) and given the potential for elevated mortality levels due to long-liners fishing for Patagonian Toothfish in this area, individual populations of this species should also be strictly monitored.

Only seven years of data exists for breeding numbers of Light-mantled sooty albatrosses on Macquarie Island and in contrast to the other three species, only a sub-sample of the breeding population was censused each year. Breeding numbers appeared stable through this time period and most inter-annual fluctuations were attributable to changes in breeding frequency. The only other published account of trends in breeding numbers of Light-mantled sooty albatrosses comes from Iles Kerguelen where the population has decreased at a rate of approximately 1-2% per annum through the 1980's and early 1990's (Weimerskirch *et al.* 1998). Very little is known about population trends of Light-mantled sooty albatrosses on other subantarctic islands and the status of large populations breeding on South Georgia and Auckland Islands remains uncertain. Recent analyses suggests that this breeding numbers have increased on Marion Island over the last decade; however, this change may reflect variation in search effort (BirdLife International, 2001b). The deficiency of data on population trends of this species makes accurate assessment of it's conservation status difficult (Gales, 1998) and further information may require that the IUCN listing is upgraded from Near Threatened to Vulnerable (BirdLife International 2001b). This species has one of the most widely distributed foraging ranges, utilising Antarctic waters during the breeding season and in light of the decreases observed at Iles Kerguelen and the increasing level of long-line fisheries in their foraging areas, monitoring of population numbers at all locations is essential.

9.3.2 Breeding success

Wandering albatrosses had the highest and most variable breeding success of all albatrosses on Macquarie Island. This variation reflects the small size of the breeding population and the impact of the failure of one or two pairs. Such variation has important implications for population trends. Successive years of low breeding success, combined with low juvenile survivorship, could severely impact on recruitment and could cause breeding numbers to decline rapidly. The high breeding success on Macquarie Island is attributable in part to pre-breeding investment in the nest and pair bond and an efficient, wide ranging and flexible foraging strategy. High chick success was also an important factor and very few chicks that hatched died over the life of the study. However, breeding success on Macquarie Island was lower than that reported at other subantarctic locations, largely due to a lower hatching success. Similar to the population and survivorship analyses, more similarities were found with geographically closer breeding populations (e.g. New Zealand and Iles Kerguelen) than with conspecifics at distant sites.

Black-browed albatrosses had the lowest breeding success of the four species on Macquarie Island. This species often forms pair and nest bonds quickly (largely as a result of its annual breeding strategy) and weaker bonds of this nature may be a significant factor in the lower hatching and overall breeding success. Chick success of this species was high and comparable with chick success of Grey-headed and Wandering albatrosses. Black-browed albatross breeding success was most similar to that observed at Iles Kerguelen and Campbell Island (*T. impavida*) and least similar to Bird Island, which probably reflects differences in the diet and foraging strategies. There was evidence to suggest that chick success and overall breeding success of this species was linked to chlorophyll A levels around Macquarie Island. However, this was a lagged correlation suggesting that pre-cursors in the marine environment for high chlorophyll A levels coincided with higher prey availability within 200 kilometres of Macquarie Island. Breeding success of Black-browed albatrosses has shown a decreasing trend since 1994/95, largely attributable to variation in hatching success and to a lesser extent chick success. This decline is most likely attributable to changes in available food resources exploited during incubation; however, the complexity of the relationship between breeding success and other parameters make it difficult to suggest single casual factors.

Breeding success of Grey-headed albatrosses showed fluctuations between 1994/95 and 2000/01 that are probably in response to fluctuating oceanic resources. The variation in hatching success and chick success contributed most equitably to overall breeding success of the three species. There was evidence that the breeding success of this species was correlated

to fluctuations in sea surface height anomalies, and that different prey were targeted in pelagic waters compared to neritic waters. There was no clear trend in breeding success of this species between 1994/95 and 2000/01. Breeding success of this species on Macquarie Island was higher than that observed in Grey-head populations at other subantarctic locations (Table 9.1) reflecting a significantly higher rate of chick success on Macquarie Island.

Overall breeding success of Light-mantled sooty albatrosses between years was most consistent of all species on Macquarie Island and this may be due to the ability of this species to utilise food resources in pelagic Antarctic waters that show less inter-annual variation in productivity. However, there was significant spatial variation in breeding success between northern and southern study sites and the mechanisms underlying this dichotomy are unclear.. There was some evidence that breeding success of this species was correlated with movement of colder water, and higher breeding success was observed when more southerly waters were closer to Macquarie Island. Further monitoring is required to assess the spatial differences in breeding success of this species on Macquarie Island.

9.3.3 Breeding frequency

The breeding frequencies of the albatrosses on Macquarie Island are consistent with conspecifics breeding at other locations (Table 9.1). Wandering albatrosses showed the strictest adherence to the biennial pattern and most Grey-headed and Light-mantled sooty albatrosses also following this pattern of breeding frequency. Approximately 20% of successful breeders from the latter two species deferred breeding for more than two years and this is probably attributable to a lack of condition in pre-breeding birds. Black-browed albatrosses followed an annual breeding pattern and the rate of deferral of breeding in this species was also likely to be related to the attainment of breeding condition in the non-breeding period.

It appears that while individual breeding quality influences breeding frequency to a certain degree there are few consistent trends between species. There is some evidence that top breeders have a greater ability to defer breeding and this is likely to be in response to environmental cues or the attainment of adequate condition in the non-breeding season. The ability to defer breeding or show more 'choice' in the breeding decision is likely to confer greater adaptive advantage and contribute to the evolution of individuals of different 'breeding quality'.

9.3.4 Attendance patterns

The mean shift lengths of albatrosses during incubation were different reflecting the primary foraging strategy of each species. Black-browed albatrosses had the shortest shift length, followed by Grey-headed, Wandering and Light-mantled sooty albatrosses. Shift length during this time period was variable, particularly for Black-browed albatrosses, indicating that breeders were foraging different distances away from Macquarie Island, or alternatively, some breeders were foraging more efficiently than others. Wandering and Light-mantled sooty albatrosses had the most similar mean shift lengths during incubation and it is likely that these two species forage almost exclusively in distant pelagic waters during this stage of the breeding cycle.

Shift lengths during the brood guard stage were significantly shorter and less variable for all four species. Foraging time during this period appears limited by the nutritional requirements of the chicks and the need to supply it with food on a regular and frequent basis. Consequently it seems likely that all albatross species on Macquarie Island utilise resources close to Macquarie Island (i.e. within 200km) during this stage of the breeding cycle. This has important ramifications for management of resources and fisheries around Macquarie Island, and should be considered in any further assessment of the Macquarie Island Marine Park boundaries.

Hatching success of Black-browed albatrosses was negatively correlated with mean shift length during early and late incubation, indicating that in years when hatching success was low, breeders tended to forage for longer periods. The mechanism behind this association may be related to changes in oceanic productivity. *Top* and *bottom* quality Black-browed albatrosses had significantly different mean shift lengths during early incubation. The ability to undertake longer shifts during this time period appears important in successfully hatching a chick and *top* quality breeders were more likely to have longer shifts in early incubation relative to late incubation. Hatching success of Grey-headed albatrosses was also negatively correlated with mean shift length in late incubation and this may be due to the movement of frontal systems and the ability of breeders to locate prey items at these systems. There was no evidence of differences in shift length between *top* and *bottom* quality Grey-headed albatrosses.

There were no negative correlations between the breeding success of Wandering albatrosses and mean shift lengths at any stage of the breeding cycle. It is likely that this species is less susceptible to changes in environmental variables and any link between attendance patterns

and breeding success are more likely to be related to aspects such as foraging zones of breeders of different age and/or experience.

9.3.5 Foraging areas of Black-browed and Grey-headed albatrosses

Black-browed albatrosses foraged primarily over neritic waters close to Macquarie Island, targeting highly productive areas above the Macquarie Island ridge complex to the north and south. However, this species also has the capacity to make long trips covering thousands of kilometres during incubation, presumably targeting food resources that are not available close to Macquarie Island. Foraging areas during the brood guard stage were similar to those targeted during incubation. There is some evidence that the foraging areas of this species are associated with high chlorophyll levels; however, bathymetry appeared to be the most influential oceanographic feature on the foraging areas targeted by this species

Black-browed albatrosses from Macquarie Island spent considerable time foraging in the Macquarie Island EEZ and CCAMLR Statistical Sub-area 88.1 and this should be considered when managing fisheries in these areas. Although the Macquarie Island Marine Park covers a large proportion of the Macquarie Island EEZ, much of the foraging time of this species is spent in areas not covered by the protected area.

Grey-headed albatrosses from Macquarie Island followed a more pelagic foraging strategy during incubation, targeting areas 1500-200 km to the east and east south-east of Macquarie Island. Different birds targeted similar areas and sea surface height anomalies were the key oceanographic feature influencing where this species foraged. During the brood-guard stage, this species foraged much closer to Macquarie Island and in a similar manner to the Black-bowed albatrosses, targeted areas over the Macquarie Island ridge complex, primarily to the south of island.

This species also spent significant amounts of time in the Macquarie Island EEZ and CCAMLR Statistical Sub-area 88.1 and this information will prove valuable in reviews of the risk assessment of this area. Grey-headed albatrosses from Macquarie Island also spent significant time foraging in the Macquarie Island EEZ that is not covered by the Marine Park protected area.

9.3.6 Chick provisioning strategies of Light-mantled sooty albatrosses

Light-mantled sooty albatrosses show a typical cyclic alternating foraging strategy during chick provisioning of a single long trip (from 5-23 days) followed by repeated short trips (up

to 3 per day) over a short space of time (2-5 days). Such a foraging strategy is typical of other pelagic Procellariiformes like the Wandering and Yellow nosed albatrosses (Weimerskirch *et al.* 1986). Foraging in this manner allows the parent to maintain its own body condition whilst satisfying the nutritional requirements of the chick.

This foraging strategy means that chicks were provisioned more sporadically than species like Black-browed and Shy albatrosses that concentrate their foraging over neritic waters. The provisioning regime of Light-mantled sooty albatrosses from Macquarie Island was similar to the Grey-headed albatross, which is consistent with the shared life history attributes of the two species. Both species also spend significant amounts of foraging time in pelagic waters. Light-mantled sooty albatrosses differed from the other species in that they delivered a consistent mean meal size regardless of the age of the chick. The amount of food each chick received was regulated by feeding frequency, particularly during the short foraging trip phases of the cycle. This strategy may allow this species to respond more efficiently to the nutritional requirements of the chick. The foraging strategy utilised appears to be the main factor influencing variation in the overall provisioning parameters.

Light-mantled sooty albatross chicks displayed a relatively typical procellariiform growth pattern with high growth rates shortly after the end of the brood guard followed by a levelling out of weight and a gradual decline as the chick approached fledging. Gompertz growth curves described the growth data well, particularly to the attainment of peak weight.

9.4 THE CONSERVATION OF ALBATROSSES ON MACQUARIE ISLAND-FUTURE DIRECTIONS

Although the population status of the albatrosses breeding on Macquarie Island have been described as currently stable there is little room for complacency. Brothers *et al.* (1999) cautioned that the threat of long-line fishing is still as present as ever before and information on the foraging areas of the Black-browed and Grey-headed albatrosses suggests that these species may be at risk from vessels fishing for Patagonian Toothfish in southern waters. The data presented here suggest that the risk assessment of CCAMLR Statistical Sub-area 88.1 may need to be upgraded in the light of this new information on foraging areas of Black-browed and Grey-headed albatrosses. Recent data from Marion Island suggested that the expanding Patagonian Toothfish fishery is impacting on population numbers in that region (Nel *et al.* 2002a; Nel *et al.* 2002b)) and given the historical similarities in the population trends of Wandering albatrosses at the two locations, it is possible that in time, similar effects will be observed on Macquarie Island.

Due to the small and vulnerable nature of Wandering, Black-browed and Grey-headed albatross breeding populations on Macquarie Island, reduction of research based human disturbance has always been a high priority throughout the current study. Therefore the low-impact, passive data collection has been and should continue to be utilised wherever possible. However, this must be balanced with the need to adequately identify and assess the risks that are facing these populations. Ground based monitoring, where breeding population numbers are assessed each year and pairs are identified, provide the minimum information required to track demographic parameters and population trends. Any monitoring of these populations in the future will benefit from the baseline data collected as part of the current study.

The critically endangered nature of the Macquarie Island Wandering albatross population provides even more incentive to minimise human disturbance to this species. Geolocation tags were deployed on five breeding Wandering albatrosses as part of the current study but due to equipment failure no valid results were obtained. Consequently, we have few specific data of the foraging areas of this species and this will need to be addressed to comprehensively assess the risks that this small population faces from external sources. Such a study will not be undertaken lightly but the success (and apparent lack of impact) of the satellite telemetry studies on Black-browed and Grey-headed albatrosses suggest that it could be undertaken successfully on this species. If one or two breeders could be successfully tracked each year for 2-3 years then over time a more complete picture of the foraging ecology could be compiled. Throughout all aspects of this study, foraging ecology has proven to be one of the critical mechanisms underlying much of the variation in demographic parameters and identifying the foraging grounds of albatrosses at all stages of the breeding cycle in identifying threats facing albatross populations. Advances in technology have enabled the foraging areas of many populations to be established (see reviews in Croxall 1998, Wilson *et al.* 2002) and as long as such research is dictated by sound conservation requirements then management strategies will benefit accordingly.

This study has examined several aspects of population demographics, breeding biology and foraging ecology of the albatrosses on Macquarie Island. The population status of each species has been assessed and major risks identified. Long-line fishing still presents a significant threat to every one of these species and for this reason all populations need to be monitored on an annual basis for the foreseeable future. Fluctuations in oceanic resources also appear to have an impact on the success and survival of these species and ongoing monitoring of these resources in the respective foraging areas should also be maintained. This study provides the first comprehensive collection of baseline data for the albatrosses breeding on

Macquarie Island and will allow monitoring studies in the future to identify any changes and assist in ensuring the long-term survival of these species.

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